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RAPID COMMUNICATION / COMMUNICATION RAPIDE

Predicting Cyanobacteria dominance in lakes

John A. Downing, Susan B. Watson, and Edward McCauley

Abstract: A controversial precept of aquatic ecology asserts that low ratios of nitrogen to phosphorus (N:P) lead to noxious and sometimes toxic blooms of Cyanobacteria. Cyanobacteria dominance is a major risk to human and ecosystem health. The stoichiometric control of Cyanobacteria therefore has become central to freshwater resource management. This controversial concept is based on observed Cyanobacteria dominance in lakes with low N:P and the results of lab and field experiments. Here we analyze data from 99 of the temperate zone's most studied lakes and show that this model is flawed. We show that the risk of water quality degradation by Cyanobacteria blooms is more strongly correlated with variation in total P, total N, or standing algae biomass than the ratio of N:P. Risks associated with Cyanobacteria are therefore less associated with N:P ratios than a simple increase in nutrient concentrations and algal biomass.

Résumé : Un précepte controversé de l'écologie aquatique veut que des faibles rapports azote:phosphore (N:P) entraînent la formation de fleurs d'eau à cyanobactéries, nocives et parfois toxiques. Une dominance des cyanobactéries constitue, en effet, un risque important pour la santé humaine et celle des écosystèmes. Le contrôle stoïchiométrique des cyanobactéries est ainsi devenu une des préoccupations principales de la gestion des ressources d'eau douce. Ce concept controversé se base sur l'observation de la dominance des cyanobactéries dans les lacs à faible rapport N:P et sur les résultats d'expériences en laboratoire et en nature. Nous analysons ici des données provenant de 99 des lacs tempérés les mieux étudiés et démontrons que le modèle est incorrect. Le risque d'une dégradation des eaux par les fleurs d'eau à cyanobactéries est en corrélation plus forte avec les variations du P total, du N total ou de la biomasse des algues qu'avec le rapport N:P. Les risques reliés aux cyanobactéries sont donc moins associés aux rapports N:P qu'à la simple augmentation des concentrations d'éléments nutritifs et de la biomasse des algues.

[Traduit par la Rédaction]

Cyanobacteria dominance in anthropogenically eutrophic lakes is an increasing problem that impacts recreation, ecosystem integrity, and human and animal health. Blooms of Cyanobacteria deposit unsightly, bad-smelling, mucilaginous clumps of dead and senescing cells on the shore and surface of lakes, impeding recreational uses. Blooms of some Cyanobacteria produce toxins during growth or decay that kill aquatic animals, and have semiochemical properties (antibiotic or allelopathic). Cyanobacterial poisoning of livestock, pets, and humans has been widely documented (Sivonen 1996). Cyanotoxins, including hepatotoxins, neurotoxins, cytotoxins, and dermatoxins (Sivonen 1996), have been linked to carcinoma and other diseases (Falconer and Humpage 1996). Cyanobacterial metabolites produce taste and odor problems that elude conventional drinking water treatment.

Remediation of these problems requires understanding the mechanisms favouring Cyanobacteria dominance in lakes. A recent review (Hyenstrand et al. 1998) lists nine mechanisms hypothesized to promote Cyanobacterial dominance in freshwaters, including resource ratio (N:P) competition, differential light requirements, CO_2 competition, buoyancy, high temperature tolerance, avoidance by herbivores, superior cellular nutrient storage, ammonium-N exploitation, and trace element competition. However, knowledge that blooms of these taxa are frequently found in nutrient rich lakes and the existence of technology to limit nutrient enrichment have made the control of Cyanobacteria by nutrients the most prominent and attractive paradigm (e.g., Reynolds 1999; Smith and Bennett 1999).

Controversy surrounds current models of Cyanobacteria dominance in surface waters. Many bloom-forming Cyanobacteria can fix atmospheric N_2 so it has been reasoned that Cyanobacteria should dominate at low N:P. This hypothesis was supported by an analysis of average seasonal data from 20 mostly northern European lakes, which concluded that ambient N:P influenced the dominance of Cyanobacteria in the phytoplankton (Smith 1983). This widely cited analysis has been debated (Trimbee and Prepas 1987) because it used

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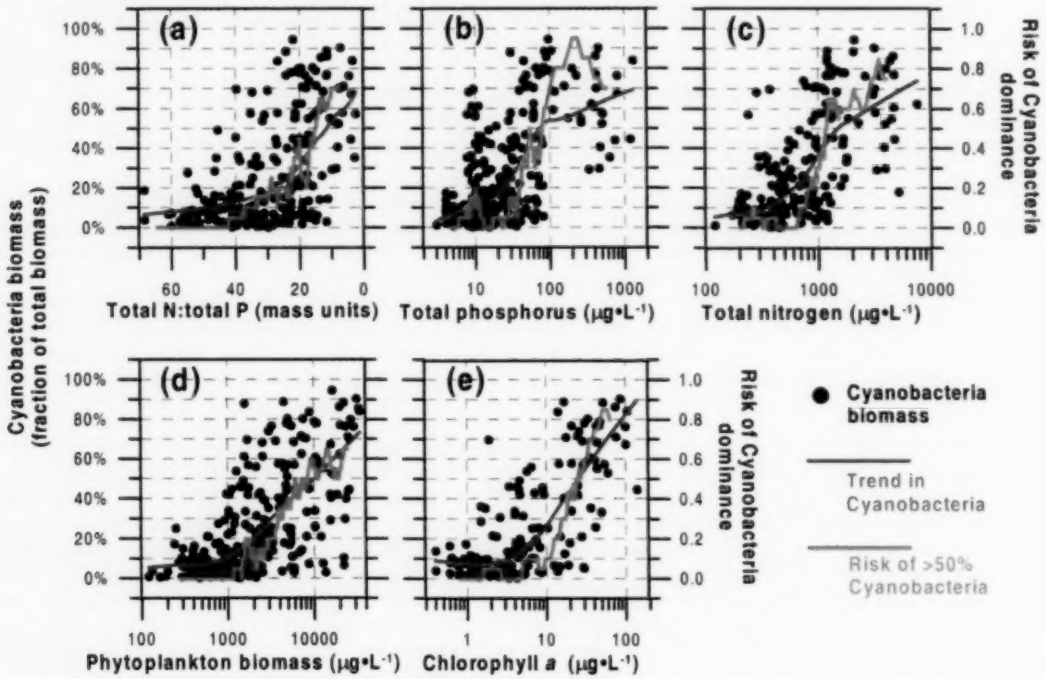
Fig. 1. The relative abundance of Cyanobacteria in the plankton of north temperate zone lakes. Dots represent the observations collected using the sources and methods indicated in the legend of Table 1. Solid lines are average LOWESS trend lines (f = 0.3, number of steps = 2) in the fraction of Cyanobacteria in the plankton (green) and the risk of plankton dominated (>50%) by Cyanobacteria (red). The risk values (see text) thus represent the fraction of world lakes with similar values of total N:total P, total P, total N, chlorophyll, or biomass that have phytoplankton composed of >50% Cyanobacteria biomass.



a small sample size, included several years' data from lakes undergoing significant changes in nutrient regime, treated data from multiple points within a lake as independent samples, and mixed data from enclosure experiments with whole-lake observations. A subsequent re-analysis (Trimbee and Prepas 1987) eliminated most of these analytical problems and suggested that nutrient concentrations (e.g., total P, total N) were better predictors of average Cyanobacteria dominance than N:P in the original dataset and another small set of lakes in Alberta, Canada. A detailed analysis of Florida lakes (Canfield et al. 1989) found only weak correlations between nutrients (concentrations or ratios) and Cyanobacteria dominance but stronger relationships of Cyanobacteria dominance with standing algal biomass. Our research seeks to discriminate between the competing hypotheses of control of Cyanobacterial dominance by nutrient stoichiometry (N:P) versus nutrient concentration (P or N) or algal biomass by using a much larger set of published data that are more representative of economically important temperate zone lakes.

We analyzed published data by synthesizing studies and reports, collecting estimates of mean ($n \geq 5$ samples) summer euphotic zone relative biomass of Cyanobacteria (as a fraction of the total phytoplankton biomass), summer mean phytoplankton biomasses measured as cell volume, and chlorophyll *a* and nutrient concentrations (total N, total P, N:P) (see most lake and data descriptions in Watson et al. (1992, 1997)). We excluded reservoirs, recently manipulated (e.g., fertilized, dredged, acidified, fish-stocked, etc.) lakes, and dystrophic brown-water lakes. Our analysis consisted of 269 observations, collected from 99 lakes around the world. Data from multiple years or sites within a given lake were included if we judged that different years or sites represented differing equilibrium conditions. No single lake dominated the data collection; the maximum representation came from 18 divergent sites and dates for Lake Ontario. None of the data included picoplankton but these small algae are generally insignificant in noxious bloom formation. Trends in the fraction of the phytoplankton community composed of Cyanobacteria were characterized using LOWESS sequential smoothing. Trends in estimates of risk of Cyanobacteria dominance were empirically calculated as the running average percent frequency of the plankton where there was an average of >50% Cyanobacteria by biomass, sequentially considering the 20 neighbouring lakes with the most similar values of the abscissa in Figure 1, i.e., total N:total P (Fig. 1*a*), total P (Fig. 1*b*), total N (Fig. 1*c*), chlorophyll *a* (Fig. 1*d*), or biomass (Fig. 1*e*). These points were plotted against the average value of the abscissa for each set of 20 lakes. The strength of correlations between these independent variables and the degree of Cyanobacteria dominance was analyzed using the "BG index" (sensu Trimbee and Prepas 1987). The BG index used as a dependent variable was calculated as $\ln(\%BG/(100 - \%BG))$, where %BG is the Cyanobacteria biomass expressed as a percentage of total phytoplankton biomass, to avoid the statistical limitations of proportional and percentage data (Trimbee and Prepas 1987).

In contrast to prevailing theory, our regression analysis of temperate zone lake data (Table 1) showed that ambient N:P

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Table 1. Efficacy of major variables for predicting Cyanobacterial abundance in temperate zone lake plankton.

Variable	Regression equation	n	RMS	r^2
Phytoplankton biomass	BG index = $-8.44 + 2.07\log_{10}$ biomass	268	1.77	0.43
Chlorophyll *a* (chloro)	BG index = $-3.10 + 1.94\log_{10}$ chloro	157	1.84	0.43
Total nitrogen (TN)	BG index = $-10.0 + 3.03\log_{10}$ TN	204	1.85	0.42
Total phosphorus (TP)	BG index = $-4.16 + 1.88\log_{10}$ TP	268	2.06	0.34
TN/TP	BG index = $3.15 - 3.29\log_{10}$ TN/TP	204	2.34	0.26

Note: Analyses were by regression. Variables and models tested were those suggested by the recent literature as most valuable for these predictions (Smith 1983; Trimbee and Prepas 1987). The data were collated from recent published studies (Watson et al. 1992, 1997) and additional data sources that are available from Dr. S.B. Watson. The BG index used as a dependent variable was calculated as $\ln(\%BG/(100 - \%BG))$, where %BG is the Cyanobacteria biomass expressed as a percentage of total phytoplankton biomass, to avoid the statistical limitations of proportional and percentage data (Trimbee and Prepas 1987). All regression analyses are statistically significant at <0.001. Although sample sizes differ among analyses, bootstrapping by randomly sampling equal numbers of observations (with replacement) showed rankings of regressions, coefficients of determination, and RMS (residual mean square error) values that are identical to those shown here. N:P impacts on Cyanobacteria do not appear to improve with consideration of light climate (see Smith and Bennett 1999) because $\log_{10}$ TP, lake depth, or water clarity (Secchi disk measurements) do not enter significantly ($\alpha < 0.05$) into a multiple regression analysis of BG index with $\log_{10}$ TN. All ambient concentrations are expressed in units of $\mu g \cdot L^{-1}$.

was the poorest predictor of Cyanobacterial dominance, compared with the trends in Cyanobacteria relative biomass with separate nutrient concentrations and total phytoplankton biomass estimates. Total P concentration alone yielded a coefficient of determination (r^2) nearly 30% larger than that of N:P. Residual mean square error estimates (RMS) show that total P yielded a prediction of Cyanobacteria relative abundance that is 12% more precise than N:P. Despite the prevalence of P limitation in north-temperate freshwater ecosystems, total N is more strongly correlated with Cyanobacteria dominance than total P. This is due to a more pronounced asymptote in Cyanobacteria dominance at high phosphorus than at high nitrogen concentrations (cf., Figs. 1*b*, 1*c*). Phytoplankton biomass is the best linear correlate of Cyanobacteria dominance, followed by concentrations of single limiting nutrients (N and P) and lastly by the ratio N:P (Table 1).

Past analyses may have perceived correlations between N:P and Cyanobacteria abundance because of a strong negative correlation between general nutrient fertility and N:P. Because rich nutrient sources are often depleted in N relative to P through biological uptake or denitrification, N:P generally declines as lakes become nutrient enriched (Downing 1997). Previous studies have shown strong collinearity between P concentrations and ambient N:P ($0.74 \leq r \leq 0.90$), making it difficult to discriminate the effects of these variables.

A main role of predictive models of Cyanobacteria dominance is to allow lake and watershed managers to manipulate nutrients to avoid conditions under which Cyanobacteria become dominant. The protection of human and ecosystem health is best served by a model that indicates conditions of highest risk of Cyanobacteria dominance with minimal misclassification of low risk conditions. This criterion is best satisfied by models that include only measurements of single limiting nutrients (e.g., total P or total N in Figs. 1*a*, 1*b*) because the right-hand sides of these graphs show few lakes with little Cyanobacteria. The N:P model does not discriminate waters where Cyanobacteria are likely to dominate from those where they do not.

The relationships shown in Table 1 provide insights of practical value. Lake managers have gained significant capabilities in managing watersheds to decrease lake water nutrient concentrations. Until now, Cyanobacteria dominance was thought to be a function of ambient N:P, with Cyanobacteria rare above N:P = 29 (by mass) but more often dominant at N:P < 29. Figure 1 shows that the relative contribution of Cyanobacteria to total phytoplankton biomass follows nonlinear relationships with phytoplankton biomass, N:P stoichiometry, and nutrient concentrations. The most potentially useful of these relationships is that with total P, because total P predicts phytoplankton biomass (Watson et al. 1992) and discriminates incisively the lakes dominated by Cyanobacteria (Fig. 1*b*). As total P increases, Cyanobacteria represent an increasing percentage of the phytoplankton biomass, rising from a minimal fraction in nutrient-poor oligotrophic lakes to an asymptotic average of 60% above total P of 80–90 $\mu g \cdot L^{-1}$.

Of greatest management importance, however, is the prediction of risk of water bodies developing phytoplankton dominated by Cyanobacteria. The risk of Cyanobacteria dominance is only 0–10% between 0 and 30 $\mu g \cdot L^{-1}$ of total P, rising abruptly to about 40% between 30 and 70 $\mu g \cdot L^{-1}$, then asymptoting at around 80% near 100 $\mu g \cdot L^{-1}$. When risk levels rise to >10%, chlorophyll *a* concentrations in the water column are >10 $\mu g \cdot L^{-1}$ (Fig. 1*d*) which often leads to a reduction in transparency to <1 m (Canfield and Bachmann 1981) and is a known breakpoint where nuisance algae blooms occur at high frequency. Therefore, there is a high likelihood that Cyanobacteria will yield a visible bloom impairment of the water body, even at P levels where the average risk of Cyanobacteria dominance is fairly low (≈20%). Lake management for minimal risk of Cyanobacteria dominance (e.g., for body-contact recreation, esthetic resources, or drinking water) requires lake total P concentrations below 30 $\mu g \cdot L^{-1}$, whereas a 40% risk of Cyanobacteria dominance (e.g., for non-contact recreation) could allow total P to rise as high as 70 $\mu g \cdot L^{-1}$. Average summer concentrations above 70 $\mu g \cdot L^{-1}$ provide an 80% guarantee of phytoplankton dominated by Cyanobacteria.

Although N:P impacts on Cyanobacterial dominance are well founded in resource-ratio theory, the stoichiometric model is of less practical value than a simpler approach based on

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single nutrients or algae biomass. This is consistent with algal biology because not all Cyanobacteria are nitrogen fixers or efficient nitrogen competitors. We show that nutrient stoichiometry plays less of a role in establishing Cyanobacteria dominance in lakes than was previously believed, and our empirical analysis suggests that we should be testing alternative explanations for dominance of Cyanobacteria. Instead, Cyanobacteria may be superior light or CO_2 competitors under turbid, CO_2-depleted conditions prevalent in nutrient-rich lakes; their photosystem and buoyancy regulation may allow them to photo-adapt to the extreme light conditions present in these systems. High temperature tolerance may allow better survival in warm, shallow, nutrient-rich environments. Avoidance by herbivores may allow them longer persistence under the intense herbivory of eutrophic lakes, or efficient ammonium-nitrogen use may allow uptake superiority in ammonium-rich eutrophic lakes. It is even possible that allelopathic exudates may favor Cyanobacteria dominance when enriched nutrients yield dense phytoplankton biomass. Studies examining ways in which combinations of these mechanisms lead to Cyanobacteria dominance are therefore of great value (Reynolds 1999).

Given the increased awareness of water quality and public safety impairment by Cyanobacteria, aquatic scientists need to emphasize prediction of their dominance in freshwater ecosystems. Although it is likely that nutrient stoichiometry influences the structure of phytoplankton communities, our analysis of temperate zone lake data shows that the key mechanisms leading to Cyanobacteria dominance may be most closely related to the physical and biological constraints accompanying a simple increase in nutrient supply.

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Effect of predation on the low-density dynamics of vendace: significance of the functional response

Outi Heikinheimo

Abstract: During the past 20 years, there have been prolonged vendace (*Coregonus albula*) recessions in several Finnish lakes. Hypotheses have been proposed that predation by brown trout (*Salmo trutta m. lacustris*) or perch (*Perca fluviatilis*) on young-of-the-year vendace could prevent the recovery of the vendace stocks from a low-density state. In this study, dynamic modelling was applied to examine the effect of predation, assuming a dome-shaped spawning stock–recruitment relationship for vendace, type II or III functional responses to predation by brown trout and perch, and a constant rate of fishing. The results showed that the form of the functional response is crucial in determining the significance of the predation on vendace stocks that have a steep dome-shaped stock–recruitment relationship. In all cases, however, predation by perch had more effect than that by brown trout, probably due to perch occupying the pelagic zone when the vendace stock is sparse. This may make the mortality of vendace increase with decreasing population density (depensatory mortality) at certain density levels.

Résumé : Au cours des 20 dernières années, il y a eu des reculs continus dans les populations de la Petite marène (*Coregonus albula*) dans plusieurs lacs de Finlande. On a posé en hypothèse que la prédation des Truites brunes (*Salmo trutta m. lacustris*) ou de la Perchaude (*Perca fluviatilis*) sur les jeunes marènes de l'année empêche vraisemblablement le rétablissement des stocks de marènes qui sont à densité faible. Notre étude utilise pour examiner les effets de la prédation une modélisation dynamique qui présume que la relation entre le stock des reproducteurs et le recrutement suit une courbe en dôme, que la prédation des Truites brunes et des Perchaudes correspond à une réponse fonctionnelle de type II ou III et que le taux de pêche est constant. Les résultats montrent que la forme de la courbe de réponse fonctionnelle est un élément essentiel pour déterminer l'impact de la prédation sur des stocks de marènes, lorsque la relation du stock des reproducteurs et du recrutement suit une courbe en dôme accentuée. Dans tous les cas, cependant, la prédation par la perchaude a plus d'effets que celle exercée par la truite, probablement parce que la perchaude occupe la zone pélagique lorsque les densités de marènes sont basses. Ceci peut avoir comme effet d'accroître la mortalité de la marène lorsque la densité de la population diminue (mortalité par effet Allee) à certains niveaux de densité.

[Traduit par la Rédaction]

Introduction

Vendace (*Coregonus albula*) is the dominant pelagic planktivore fish species in many Finnish and other northern European lakes. Large variations in year-class strength are typical of vendace stocks (Viljanen 1986; Salojärvi 1987; Auvinen 1994). The unpredictability of the coming yields poses a serious problem in the exploitation of vendace, the most important target species of commercial fishing in Finnish inland waters (Sipponen et al. 1999).

During the past 20 years, there have been prolonged recessions in the vendace stocks in several lakes (Valkeajärvi et al. 2001), e.g., Lake Konnevesi (Valkeajärvi and Bagge 1995), Lake Puruvesi (Karjalainen et al. 2000), Lake Puula (Marjomäki et al. 1995), and Lake Pyhäjärvi (Helminen et al. 1997). In Lake Päijänne, a period of low vendace recruitment lasted from 1983 to 1995. There is agreement on the importance of the larval and juvenile mortality in determining the strength of the recruiting year-class (e.g., Viljanen 1986; Auvinen 1994; Karjalainen et al. 2000). Most of the mortality usually occurs in the critical phase of the early larval period. However, the final strength of the recruiting year-class is determined during the juvenile phase in the first summer (Helminen and Sarvala 1994).

Brown trout (*Salmo trutta m. lacustris*), the predominant salmonid predatory fish in the pelagic zone, is commonly stocked into Finnish lakes. Therefore, debate has been raised about the possible role of brown trout in the fluctuations of the vendace stocks, especially in maintaining a low-density state. Consequently, recommendations have already been given to restrict brown trout stocking (e.g., Helminen et al. 1997; Vehanen et al. 1998). Similar concerns were presented on the effect of predatory fish stocking on the prey species in the Great Lakes (Jones et al. 1993; Kitchell et al. 1994).

On the other hand, assumptions have been presented that perch (*Perca fluviatilis*), as a predator of young-of-the-year vendace, may play a role in the dynamics of vendace stocks. This is because a high abundance of perch has been observed in the pelagic zone during periods of low vendace density (Auvinen 1994; Helminen and Sarvala 1994; Valkeajärvi and Bagge 1995).

There have been several attempts to estimate the effect of predation by brown trout on vendace stocks (e.g., Vehanen et al. 1998), but the effect of prey density on the predation rate

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(functional response) was not taken into account, except by Marttunen and Kylmälä (1997) and Heikinheimo et al. (2001). Further, most of these attempts are principally based on an equilibrium assumption. This assumption may only be relevant during long recession periods, where the recruitment is relatively even. There are apparently several interacting mechanisms behind the fluctuations in vendace stocks, such as the stock–recruitment (S/R) relationship, predation, competition, and fishing (e.g., Hamrin and Persson 1986; Salojärvi 1987; Helminen et al. 1997). Modelling studies are needed to consider the resultant complex dynamics (Salojärvi 1987; Heikinheimo et al. 2001).

The main reason why predation is seldom included in fish stock models is the lack of sufficient data to estimate the parameter values (Hilborn and Walters 1992). However, in spite of uncertainty of the parameters, a model can increase our understanding if the basic mechanisms can be outlined and incorporated into the model. Simple models are valuable in assessing the general plausibility of particular mechanisms (Hanski and Korpimäki 1995) and effective tools for studying such basic properties of a dynamic system as stability and limit cycles, which are the basis for understanding ecological systems (DeAngelis 1988). Another advantage is that the model may reveal the points that are crucial in the dynamics and thus need more attention in the research. Ignoring important factors leads more probably to erroneous conclusions and management advice than incorporation of uncertain information into the model (Hildén 1997).

The goal of this study was to examine the effect of predation on the dynamics of vendace stocks, in particular to (*i*) determine if the predation could in some circumstances cause or maintain low-density states in the vendace, (*ii*) examine the significance of the functional response in the low-density dynamics of vendace, and (*iii*) determine which variables are important in assessing the effect of predation on vendace and therefore need more attention in future research. A simple dynamic model was constructed to simulate the effects of, according to the current hypotheses, the most important predators on vendace with different alternatives of the S/R relationship.

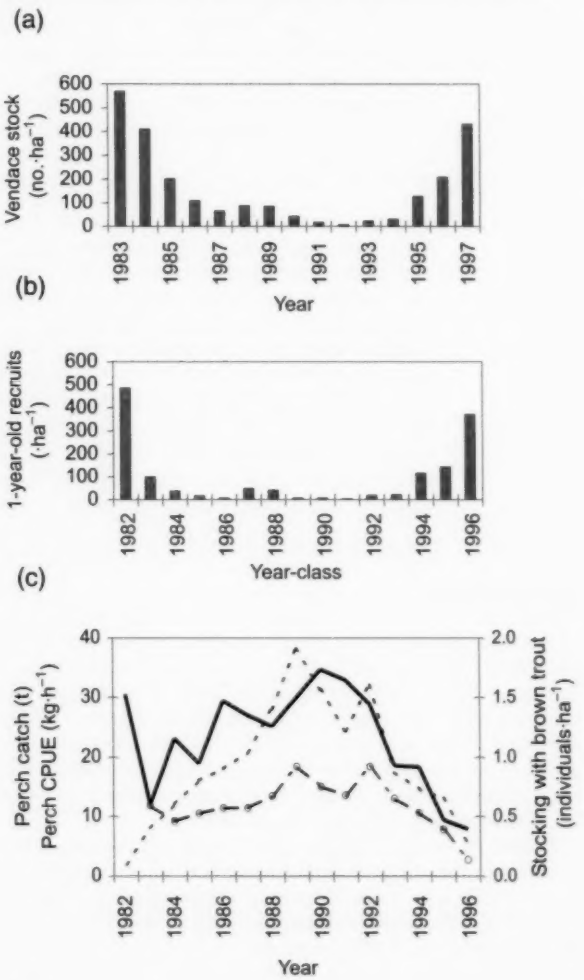
Material and methods

Vendace, brown trout, and perch in Tehinselkä, Lake Päijänne

Tehinselkä is the largest open-water area in Lake Päijänne, with a surface area of 200 km^2. Most of the commercial vendace fishery of the lake is concentrated in this area (Valkeajärvi and Salo 2000). Lake Päijänne presents an example of a long recession of the vendace stock (Valkeajärvi et al. 1997). The vendace stock was strong or moderate in the late 1960s. During the 1970s, there was a long period of lower than average stock size until a strong year-class was born in 1982. This was followed by a period of low recruitment until 1996 when the first abundant year-class was born (Fig. 1).

The density of the vendace stock (1-year-olds and adults) in Tehinselkä, calculated from the catch data (P. Valkeajärvi, Finnish Game and Fisheries Research Institute, Laukaa, Finland, unpublished data) using cohort analysis with Pope's method (e.g., Hilborn and Walters 1992), was at the level of 600·ha^{-1} at the highest and varied from 10 to 100·ha^{-1} during the lowest densities. The stocking density of brown trout, calculated as 2-year-old smolts, was

Fig. 1. Vendace (*a*) stock density and (*b*) annual recruitment in Tehinselkä, Lake Päijänne, calculated from the data on trawl catches of vendace from 1983 to 1996 (Valkeajärvi and Salo 2000; P. Valkeajärvi, Finnish Game and Fisheries Research Institute, Laukaa, Finland, unpublished data) using cohort analysis and (*c*) stocking of brown trout (solid line), the perch catch from trawls from 1982 to 1996 (dashed line), and the trawl catch per unit of effort (CPUE) of perch from 1983 to 1996 (dashed line with circles). The perch catch from 1982 to 1989 was not reported separately but is estimated at 40% of the total catch of species other than vendace and whitefish. The number of stocked brown trout is converted to 2-year-old smolts (Heikinheimo et al. 2001).



high (0.6–1.7·ha^{-1}) from 1982 to the early 1990s and decreased to about 0.4·ha^{-1} in 1996 (Fig. 1) (Valkeajärvi et al. 1997).

The trawl catch of perch in Tehinselkä was at a very low level in 1982 when the vendace stock was dense and then rose during the 1980s, being at its highest in 1989 at 38 t (2 kg·ha^{-1}). After that, the catch decreased again, reaching 5.6 t in 1996 and 3 t in 1997. The catch per unit of effort shows a similar trend (Fig. 1) (Valkeajärvi and Salo 2000).

In Lake Päijänne, the young-of-the-year vendace were the most

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important food item for 2- and 3-year-old brown trout in 1996 (the year of high recruitment) and made up nearly 100% of the diet when of optimal individual size (Koivurinta et al. 2000; Heikinheimo et al. 2001). This is in contrast with 1995 when the density of the young-of-the-year vendace was low and substantially fewer were taken by brown trout. The young-of-the-year vendace were most vulnerable to predation by brown trout at a size of 4–8 cm. Hence, the duration of the effective predation depends on the growth of the vendace juveniles.

There are no data on the food of perch in Lake Päijänne, but young-of-the-year vendace were found in most perch stomachs taken at the end of June in 1998 (T. Marjomäki, University of Jyväskylä, Jyväskylä, Finland, personal communication). In Lake Puruvesi, the perch that fed on vendace juveniles in the pelagic zone were mostly 17–22 cm in length (Jaatinen et al. 1999). Vendace was insignificant in the food of perch during the vendace recession in Lake Puruvesi when the autumn density of young-of-the-year vendace was near zero. In 1995, when the vendace stock started to recover, 59% of the pelagic perch used vendace as a predominant food species (Jaatinen et al. 1999). The size of vendace juveniles taken by perch was smaller (monthly mean length 3–6 cm, 0.2–1.2 g in weight) than the average size (3–8 cm) in the pelagic phase. This is in accordance with the results from Lake Konnevesi, where the perch favoured prey fish less than 5 cm in length and the predation on vendace was strongest in June and July (Tolonen 2000).

Structure of the model, basic assumptions, and equations

Vendace model

The vendace model (Fig. 2*a*) includes three age-classes: young-of-the-year vendace, 1-year-olds, and adults. The vendace enter the next age-class at the beginning of each year. The spawning stock consists of 1-year-olds and adults. The strength of a new year-class, in numbers of 0+ vendace in the beginning of the pelagic phase (June 1), depends on the spawning stock biomass (age groups 1 or older) through an S/R relationship according to Shepherd's (1982) equation:

$$(1)\quad R = aS/(1 + (S/K)^b)$$

where R is the number of recruits, S is the spawning stock biomass (kilograms per hectare), K is the threshold biomass of the spawning stock (kilograms per hectare), and a and b are constants. Hence, the larval mortality is embedded in the S/R relationship. The S is calculated as $N_1w_1 + N_aw_a$, where N_1 is the number of vendace per hectare in age group 1 at the end of September, w_1 is the mean weight of 1-year-old vendace (15 g), and N_a and w_a (80 g) are the parameters for adult vendace. Constant average weights were used in the model. In reality, the growth rate of vendace varies and is generally density dependent (Salojärvi 1987), but the data from Lake Päijänne were collected during a period of sparse population. The annual mean weights of 1-year-old vendace in Lake Päijänne ranged from 6 to 21 g (P. Valkeajärvi, Finnish Game and Fisheries Research Institute, Laukaa, Finland, unpublished data). The annual mean weight of adult vendace in the trawl catch varied from 40 to 120 g.

The rate of change in stock size in each age-class during the year is modelled according to the equation

$$(2)\quad \mathrm{d}N/\mathrm{d}t = -ZN$$

where N is the stock size (numbers per hectare) in the age-class in question and Z is the instantaneous rate of total mortality per year. At age 1 and in adult vendace, $Z = F + M$, where F is the rate of fishing mortality and M is the rate of natural mortality. The causes of natural mortality were not separated in these age groups. The 0+ vendace experience mortality through predation by brown trout and perch but are not yet recruited to the fishery. The rate of predation depends on the density of 0+ vendace through a functional response, and the instantaneous predation mortality caused by a predator species is linearly dependent on the number of predator individuals.

The functional response is the number of prey consumed per predator per unit of time as a function of prey density (Holling 1959; Murdoch 1973; Taylor 1984). The simplest assumption, commonly applied in fish stock assessment, is a constant instantaneous natural mortality, which means a linear functional response. More probably, the number of prey taken in a unit of time increases with prey density at a decelerating rate approaching an asymptote (Murdoch 1973). This response (type II) causes prey mortality that is inversely density dependent (Fig. 3). There could also be a lower limit of prey density, where the predation ceases due to, for instance, shifting to more available prey species (Murdoch 1973). This would result in a sigmoid curve for the functional response (type III) and density-dependent mortality of the prey at a range of low densities (Fig. 3). These alternative types of functional response were used in the model in separate runs.

Hence, the number of 0+ vendace eaten by one brown trout in a unit of time is the functional response (R_b). The equation for the type II functional response (Fig. 3) is

$$(3)\quad R_b = C_{\max,b}N/(N + D_b)$$

and that for the type III functional response (Fig. 3) is

$$(4)\quad R_b = C_{\max,b}N^2/(N^2 + D_b^2)$$

where $C_{\max,b}$ is the maximum consumption by one brown trout in the unit of time, N is the number of 0+ vendace per hectare, and D_b is the half-saturation constant or the number of 0+ vendace per hectare when the consumption by one brown trout is half the maximum.

Because the proportion of 0+ vendace eaten by one brown trout is very small, it equals the instantaneous predation mortality caused by one brown trout (m_b):

$$(5)\quad m_b = R_b/N$$

and hence, the predation mortality caused by the brown trout population (M_b) is

$$(6)\quad M_b = BR_b/N$$

where B is the number of brown trout.

The predation mortality by perch (M_p) is modelled similarly, and hence the total instantaneous mortality Z of 0+ vendace in eq. 2 is $M_b + M_p$.

Brown trout model

The brown trout model is very simple, with no age structure and constant natural and fishing mortalities (Fig. 2*b*). Given the present fishing mortality, 2- and 3-year-old brown trout are the main age groups in the population (Heikinheimo et al. 2001) and are more important as predators of the 0+ vendace than the older ages (Koivurinta et al. 2000). In the model, the brown trout are stocked as 2-year-old smolts at the beginning of June in constant numbers (B_s). The poststocking mortality is A, and hence, the number surviving from stocking (B_0), which joined the population on June 1, is

$$(7)\quad B_0 = (1 - A)B_s$$

The rate of change in the stock size in numbers (B) is

$$(8)\quad \mathrm{d}B/\mathrm{d}t = -(F_b + M_b)B$$

where F_b and M_b are the instantaneous rates of fishing and natural mortality, respectively.

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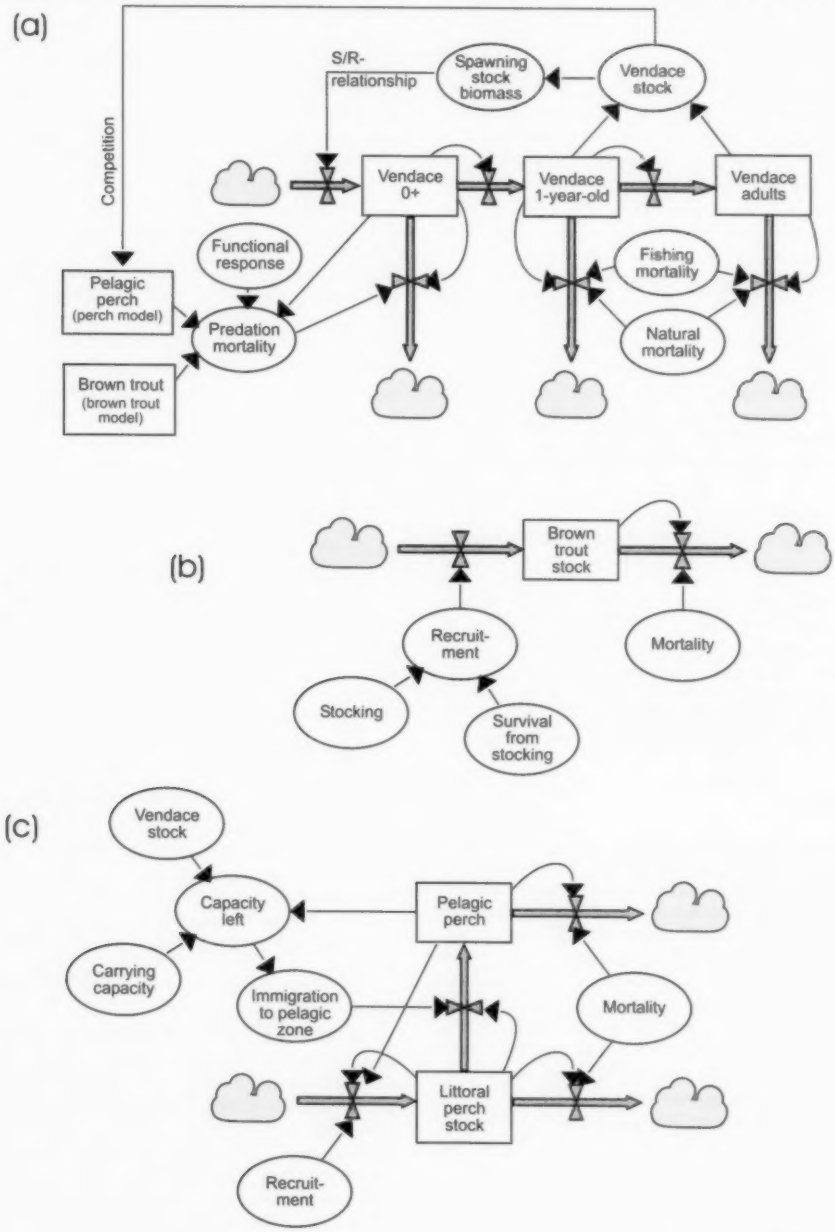
Fig. 2. Structure of the dynamic model describing the interaction between vendace, brown trout, and perch with three submodels: (*a*) vendace model, (*b*) brown trout model, and (*c*) perch model. Squares, level variables (numbers of fish); ovals, auxiliary variables. Arrows between the level variables (or between a level variable and a "cloud") indicate flows (in numbers of fish), with faucets that regulate the flows; thin arrows indicate effects on variables or flows. The "clouds" represent the borders of the system.



Perch model

In the perch model (Fig. 2*c*), the stock is not divided into age groups, and it only represents the adult stock (>17 cm), which are potential predators of vendace. The perch stock is assumed to be in equilibrium (recruitment equals mortality). The abundance of perch year-classes is affected mainly by spring and summer temperatures (Lehtonen and Lappalainen 1995), but such cyclic variation as in vendace, for instance, is not known in perch stocks. In the model, the recruitment of perch takes place in the littoral zone, but there is a subpopulation in the pelagic zone. The recruitment is modelled as a constant process (rate r_p) on the basis that the perch stock consists of several year-classes with differing growth rates, and thus, there would be a gradual recruitment to the size-class potentially feeding on 0+ vendace. The total mortality (Z_p) is not divided into separate components.

The density of perch tends to increase in the pelagic habitat when the vendace stock is sparse (Auvinen 1994; Valkeajärvi and Bagge 1995), whereas vendace has the ability to edge out other

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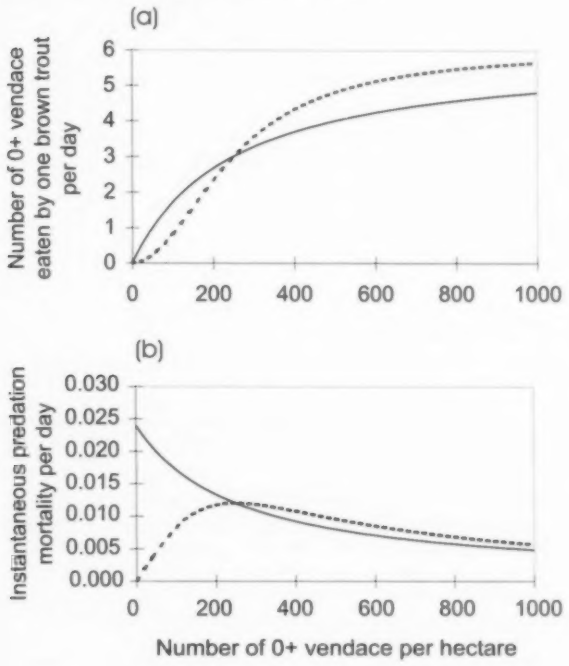
Fig. 3. (*a*) Functional response curves of type II (solid line) and type III (dashed line) used in the model for the predation by brown trout on 0+ vendace and (*b*) the corresponding instantaneous rates of predation mortality. The half-saturation constant (D) is 250 0+ vendace per hectare in both types, with a maximum consumption of six vendace per day.



species when it is at high densities (Svärdson 1976). Thus, in the model, the rate of immigration of perch from the littoral population to the pelagic zone depends on the density of the littoral perch stock and is restricted by the density of the vendace stock. There is intraspecific competition in the perch population as well because the growth of perch is density dependent (Raitaniemi et al. 1988). This can be described by means of a carrying capacity in terms of the combined density of pelagic perch and vendace, which restricts the density of the pelagic perch substock but not that of the vendace. In the model, the perch enter the pelagic zone at an instantaneous rate (E), which is restricted by the carrying capacity K_p. Hence, the change in the total density of perch is given by

$$(9)\quad dP/dt = (r_p - Z_p)P$$

The rate of change in the littoral stock (P_{litt}) is expressed as

$$(10)\quad dP_{litt}/dt = r_pP - Z_pP_{litt} - EP_{litt}(1 - (N_v + P_{pel})/K_p)$$

and the rate of change in the size of the stock in the pelagic zone (P_{pel}) as

$$(11)\quad dP_{pel}/dt = EP_{litt}(1 - (N_v + P_{pel})/K_p) - Z_pP_{pel}$$

with the condition if $(N_v + P_{pel}) > K_p$, $E = 0$, where E is the immigration rate into the pelagic zone, Z_p is the instantaneous total mortality of perch, N_v is the size of the vendace stock in numbers (1-year-olds and adults), and K_p is the carrying capacity for perch in the pelagic zone.

Parameter values

S/R relationship for vendace

There is abundant evidence on dome-shaped S/R relationships in vendace stocks (e.g., Salojärvi 1991; Salmi and Huusko 1995). The results of the cohort analysis from Lake Päijänne suggest that the vendace year-classes from 1983 to 1995 were weak, and only the year-classes 1982 and 1996 were strong (Fig. 1). Hence, there was only one dense year-class (1996) for which the density of the spawning stock could be calculated (Fig. 4). To develop the parameters for the S/R curve (0+ recruits), it was assumed that the density of 0+ vendace would be 1.5 times the density of 1-year-old fish, calculated with cohort analysis (Fig. 4). The highest point of the curve would then be about 600·ha^{-1}. During the first summer, the predation takes a larger proportion from sparse year-classes than from the dense ones (Vehanen et al. 1998), and hence, the densities of 1-year-old recruits yield a steeper S/R curve than those of the 0+ recruits. The best parameters of Shepherd's equation for 0+ recruits would be, given the data and the assumptions mentioned above, $a = 330$, $b = 3$, and $K = 3.5$ kg·ha^{-1} (Table 1; Figs. 4 and 5). Because of the uncertainty of the S/R relationship, several alternative curves with differing steepness (lower values for a or b) were used in the model (Fig. 5).

Stocking of brown trout

The stocking density of brown trout in Lake Päijänne, estimated as 2-year-old smolts per hectare of open lake area deeper than 10 m, ranged from 0.3 to 1.7 individuals·ha^{-1} during the period 1982–1996 (Fig. 1). Two-year-old smolts (150 g in weight) were routinely used in stocking, but during the 1990s, 3-year-olds (400 g) and even older brown trout were released. In the model, a stocking density of 1.2·ha^{-1} was used as a nominal value (Table 1), representing the high stocking level during the 1980s and 1990s (Fig. 1). The stocking was assumed to occur at the start of June every year. To simulate the effect of a larger stocking density, a double value was used (2.4·ha^{-1}).

Parameters in the perch model

The density of the perch stock in the pelagic zone was estimated on the basis of the trawl catches. This was done by considering vendace population and catch in numbers on the basis of the vendace population model by Heikinheimo et al. (2001) and extrapolating their relationship to perch. For vendace, the population size was more than twofold the catch in numbers when the instantaneous rate of natural mortality was 0.1–0.3 and the rate of fishing mortality was 0.6. The perch catch in numbers was at the highest 1.3 million, and the corresponding population size was estimated at about 3 million (150·ha^{-1}). If the fishing mortality had been lower, 0.4 for instance, the population size would have been nearly fourfold compared with the catch in numbers (5 million, 250·ha^{-1}).

Because the perch population was at its densest during a period of very sparse vendace stock, we may assume that the combined vendace and perch density during that time represents the highest possible density in the pelagic habitat. In 1989, the stock size of vendace at the beginning of the year was about 100·ha^{-1}, and the density of the perch stock was earlier estimated at 150–250·ha^{-1}. The value of K_p in the model was set to 700·ha^{-1} (Table 1), which allows the density of perch to rise to a maximum level of 400·ha^{-1} at low vendace densities.

A constant instantaneous total mortality was assumed for perch ($Z_p = 0.5$, Table 1), which is lower than that of vendace (0.9) on the basis that the catchability by trawl is probably lower. The rate of recruitment was assumed to be equal to the mortality rate to keep the perch stock in equilibrium. The nominal value of the maximum rate of immigration to the pelagic zone is 0.3 (Table 1), which allows the perch to occupy the pelagic zone in a few years during low vendace density.

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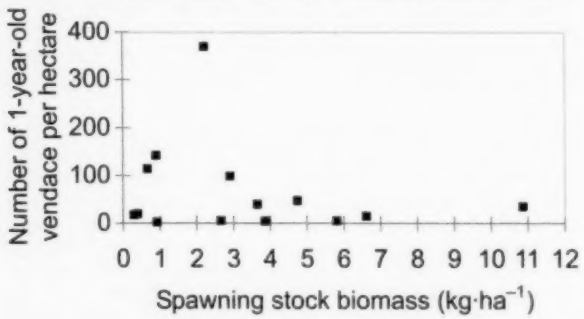
Table 1. Model parameters and the nominal values used in the simulations (limits of random variation in parentheses).

Parameter		Value	Source(s)[a]
Vendace model			
a	Parameter in the S/R equation for vendace	330	1
b	Parameter in the S/R equation for vendace	3	1
K	Threshold biomass in the S/R equation for vendace (kg·ha^{-1})	3.5 (2.5–4.5)	1
D_b, D_p	Half-saturation constants in the equation for the functional response in predation by brown trout and perch (0+ vendace·ha^{-1})	250	2
$C_{max,\ b}$	Maximum consumption (in numbers) of 0+ vendace by one brown trout per year	720	2, 3
$C_{max,\ p}$	Maximum consumption (in numbers) of 0+ vendace by one perch per year	15	4
F	Annual instantaneous rate of fishing mortality in 1-year-old and adult vendace	0.6	1
M	Annual instantaneous rate of natural mortality in 1-year-old and adult vendace	0.3 (0.1–0.5)	2
Brown trout model			
B_s	Number of brown trout smolts stocked annually per hectare	1.2	2
A	Poststocking mortality	0.5	2
Z_b	Annual instantaneous rate of total mortality	1.5	2
Perch model			
r_p	Annual instantaneous rate of recruitment	0.5 (0.4–0.6)	5
Z_p	Annual instantaneous rate of total mortality	0.5	5
E	Annual instantaneous rate of immigration to the pelagic zone	0.3	5
K_p	Carrying capacity in terms of density of pelagic perch and vendace (no.·ha^{-1})	700	5

[a]1, Calculated on the basis of unpublished data by P. Valkeajärvi (Finnish Game and Fisheries Research Institute, Laukaa, Finland); 2, Heikinheimo et al. (2001); 3, Koivurinta et al. (2000); 4, calculated on the basis of Jaatinen et al. (1999); 5, see text for explanation.

Fig. 4. Numbers of 1-year-old vendace in Tehinselkä, Lake Päijänne, from 1983 to 1996 plotted against spawning stock biomass calculated from the data of P. Valkeajärvi (Finnish Game and Fisheries Research Institute, Laukaa, Finland, unpublished data).



Parameters of the equation for the functional response

Predation by brown trout on 0+ vendace—The maximum consumption of 0+ vendace by brown trout, as the average number of 0+ vendace eaten per day by one brown trout, was calculated from the data on the diet of 2- to 4-year-old brown trout by Koivurinta et al. (2000). The data were from 1996, when a strong year-class of vendace was born in Lake Päijänne. The food consumption of brown trout was estimated with a bioenergetics model (Heikinheimo et al. 2001). The average value was six individuals per day. The predation on 0+ vendace ceases when they exceed the optimal size for predators, which was 7–10 cm for brown trout in Lake Päijänne (Koivurinta et al. 2000). In this model, the vendace were assumed to reach this size in 4 months (120 days) after entering the pelagic zone at the beginning of June, and the predation by brown trout is restricted to this period (predation time). Thus, the maximum consumption during this period was 720 individuals per one brown trout (Table 1).

Heikinheimo et al. (2001) estimated the value of the half-saturation constant D at 250–500·ha^{-1} for the predation by brown trout on 0+ vendace in Lake Päijänne, assuming a type II functional response, and the maximum consumption was equal to the consumption in 1996. The lower value (D = 250·ha^{-1}) was used here in both type II and III functional responses (Table 1).

Predation by perch on 0+ vendace—In Lake Puruvesi, perch were estimated to have consumed 1600 0+ vendace per hectare in 1996 (Jaatinen et al. 1999). This was the year when the density of the vendace year-class in the autumn was about 1000·ha^{-1}, and the density of the perch population in the pelagic zone was estimated at 5.5 kg·ha^{-1} (183 individuals·ha^{-1} if the mean weight was 30 g or 137 individuals·ha^{-1} if the mean weight was 40 g). The number of vendace eaten by one perch in one year would be 9–12. The optimal size of vendace is even smaller for perch than for brown trout (Jaatinen et al. 1999), which means that the predation by perch is restricted to a short period. In this model, the maximum consumption by one perch per year was assumed to be 15 vendace and the predation period 2 months (Table 1). The functional response in the perch–vendace relationship is not known. Therefore, the same value of D used for brown trout in the model was used for perch, too.

Analysis strategy

Powersim® 2.5 for Windows was used to construct and run the model, and Euler's integration method was used in the simulations, with 1 year as the unit of time and 0.01 year as the time step. The model was run for 200–300 years in each case.

The model was first run with constant parameter values, starting from three hundred 1-year-old vendace per hectare, other age-classes of vendace being at zero. Other starting values from 10 to 1000 were tested also to determine if the results were affected. The starting value for the littoral perch stock was 1000·ha^{-1} (calculated per hectare of pelagic area), with no perch in the pelagic zone. The starting value for the brown trout stock was zero. The model was run with constant fishing and natural mortalities in the adult vendace and different combinations of predation on 0+ vendace: no

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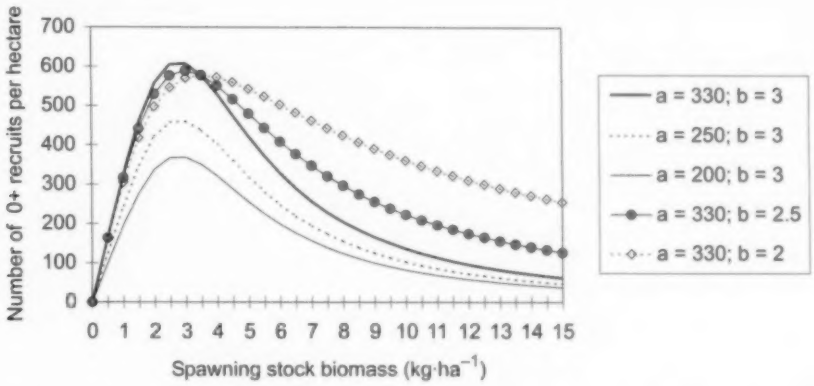
Fig. 5. Alternative spawning stock – recruitment curves for 0+ recruits used in the simulations. The most probable (nominal) parameter values are $a = 330$ and $b = 3$.



predation, predation by brown trout but no perch, predation by perch but no brown trout, and predation by both species. The natural mortalities in the other age-classes of vendace were constant. The effect of the S/R relationship was examined by using alternative values for a and b in the equation (Fig. 5). This set of runs was done first using the type II functional response and then using the type III response with the same parameter values.

Second, to simulate the natural situation more realistically, random variation with uniform distribution was incorporated into the following parameters: K (threshold biomass for the spawning stock of vendace), the rate of recruitment of perch, and the natural mortality of adult vendace. The ranges of variation are given in Table 1. The parameter values were made to vary only between years, the rates being constant during each year. The random variation was kept identical in each run by giving a seed number in the first simulation. Hence, the density of the pelagic perch varied within the range allowed by the carrying capacity in the perch model. The effect of predation by brown trout was studied by changing the stocking density, and similar runs were again done using both types of functional response, assuming the nominal S/R relationship. In another set of runs, the level of brown trout stocking was made to decrease stepwise, and this was repeated for both types of functional response and different S/R relationships. The effect of the rate of fishing was not examined in this study.

Results

Effect of the S/R relationship and the type of functional response

The model was first run with constant parameter values without random variation, with the density of the vendace stock per hectare (1-year-olds and adults) as the output variable.

Type II functional response

With the nominal parameter values ($a = 330$, $b = 3$) in the S/R relationship, a regular cycle in the vendace stock is produced, with an amplitude from 205 to 618 individuals·ha^{-1} and a period of 6–7 years (mean 6.25) (Fig. 6; Table 2). Predation by brown trout with a stocking density of 1.2·ha^{-1} increases the amplitude of oscillation by about 100·ha^{-1}, with higher maximum and lower minimum values. Doubling the stocking density causes only a slight difference in the model output compared with that produced by the standard stocking density. The mean level of the density of the vendace stock is then about 40·ha^{-1} lower. Predation by perch affects the fluctuation pattern more than that by brown trout, the maximum values and the amplitude of oscillation being lower, from 113 to 442·ha^{-1}. The period in the oscillation also increases slightly (mean 6.45). When both predators are acting simultaneously, the amplitude decreases because of lower peaks in the oscillation. In this scenario, starting densities of forty 1-year-old vendace per hectare or lower lead to a different output, the density of vendace converging rapidly towards zero.

The alternative S/R relationships with lower values for a and b lead in most cases to an equilibrium point or a cycle converging to an equilibrium (Table 2). The less steep forms of the S/R relationship (low b values) lead to higher equilibrium levels, and in these cases, the relative effect of the predation by brown trout is larger than in the case with the nominal values for a and b. Low values of a increase the probability of the vendace stock falling to zero.

Type III functional response

The overall picture of the behaviour of the model with the type III response is more stable than with the type II response (Fig. 7; Table 2). The oscillation is converging towards an equilibrium point in each case of predation. With the nominal S/R curve, the brown trout stocking has a clearer effect on the vendace stock density than with the type II response. On the other hand, there is only a small difference (30·ha^{-1}) between the case with perch predation only and the case with both predators. The vendace stock does not fall to zero in any case, even if the simulation was started from low densities. With flat S/R curves ($b = 2.5$ or 2), the equilibrium densities of vendace are almost equal irrespective of the type of functional response, with the exception that with the type II response, low starting values lead to zero output.

Type II functional response for brown trout and type III for perch

The simulation results with both predators are very similar to the preceding case with the type III response for both predators (Table 2). As in that case, with the nominal S/R curve, the perch predation alone would have almost the same

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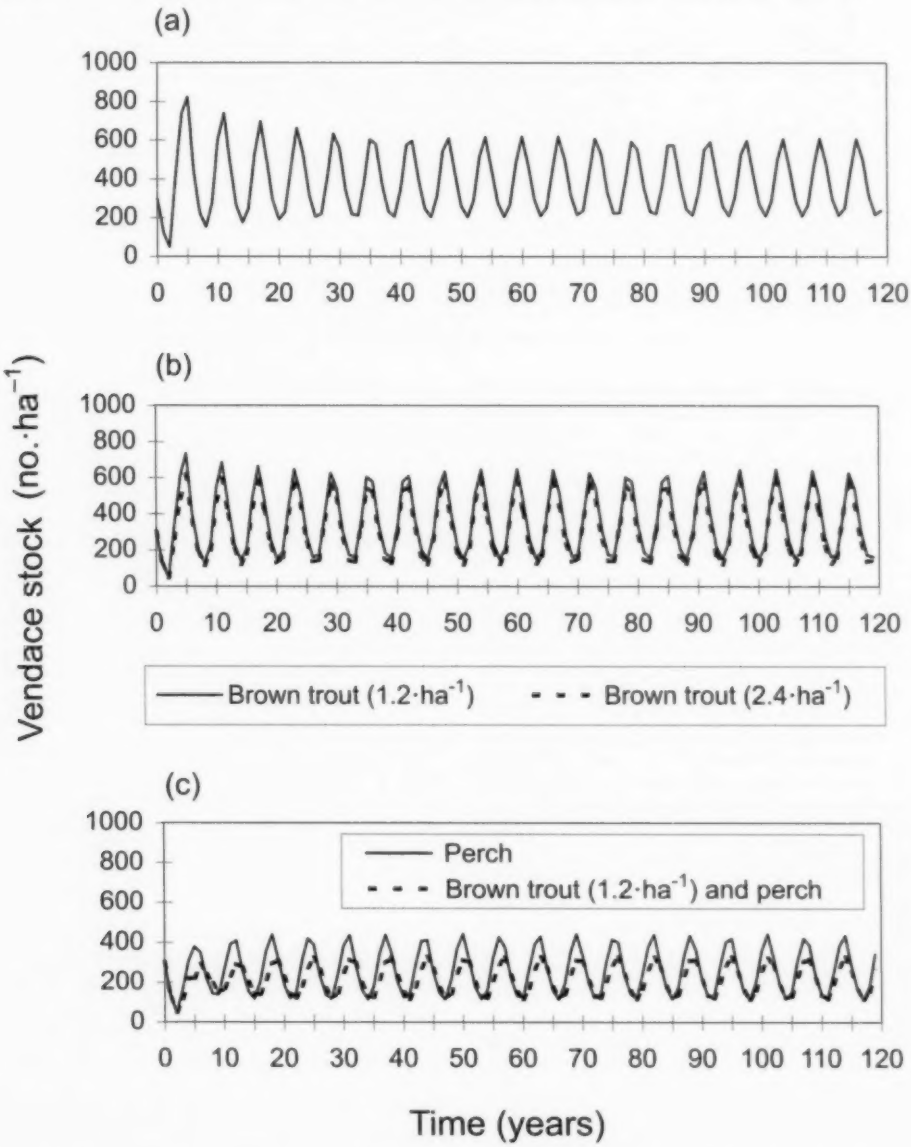
Fig. 6. Results of model simulations with constant parameter values assuming the type II functional response and the nominal S/R relationship (a = 330, b = 3). Densities of the vendace stock (1-year-olds and adults) for different predation scenarios: (a) no predation on 0+ vendace, (b) predation by brown trout only, and (c) predation by perch only and predation by both species.



effect as the combined perch and brown trout predation. In this case, the predation by brown trout alone would not markedly affect the equilibrium densities of vendace compared with the situation with no predation on 0+ vendace.

Random variation in key parameters and changing predation pressure

Effect of perch

Type II functional response—In the first simulation, the stocking density of brown trout was 1.2·ha^{-1}, and the pelagic perch population varied from 200 to 410 individuals·ha^{-1}, showing an increasing trend during years 50–100 (Fig. 8*a*). From year 120 onwards, the mortality of perch was increased to 0.6 to make the density of perch decrease slowly. The resulting density of the vendace stock shows irregular fluctuation within the range of about 50–300·ha^{-1}, with some periodicity. The density of the vendace stock and the range of fluctuation decrease with increasing perch density, converging towards zero when the density of pelagic perch exceeds 400·ha^{-1}. In nature, this would mean an extinction of the vendace, but in the model simulation, the vendace stock recovers even from very close to zero when the perch stock is

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Table 2. Results of model simulations with constant parameter values for different S/R curves, predation scenarios, and type II and III functional responses.

(A) Type II functional response.

Parameter values of the S/R curve	Dynamics	Predation on 0+ vendace				
		No predation	Brown trout at 1.2·ha^{-1}	Brown trout at 2.4·ha^{-1}	Perch	Brown trout (1.2·ha^{-1}) and perch
a = 330, b = 3	6- to 7-year limit cycle					
	Mean	382	358	319	264	219[a]
	Min.–max.	205–618	150–648	122–588	113–442	116–328
a = 250, b = 3	6- to 7-year limit cycle					
	Mean	—	298	260	206	171[b]
	Min.–max.	—	171–458	148–396	177–235	170–172
	6- to 7-year damping cycle, mean	329	—	—	—	—
a = 200, b = 3	6- to 7-year damping cycle, mean	298	261	—	—	—
	Equilibrium point	—	—	226	172	—
	Converging to zero	—	—	—	—	Yes
a = 330, b = 2.5	6- to 7-year damping cycle, mean	421	371	326	—	—
	Equilibrium point	—	—	—	276	234[a]
a = 330, b = 2	Equilibrium point	535	465	401	343	276[a]

(B) Type III functional response.

Parameter values of the S/R curve	Dynamics	Predation on 0+ vendace					
						Brown trout (1.2·ha^{-1}) and perch	
		No predation	Brown trout at 1.2·ha^{-1}	Brown trout at 2.4·ha^{-1}	Perch	Both species type III	Brown trout type II
a = 330, b = 3	6- to 7-year limit cycle						
	Mean	382	—	—	—	—	—
	Min.–max.	205–618	—	—	—	—	—
	6- to 7-year damping cycle, mean	—	325	289	—	—	—
	Equilibrium point	—	—	—	248	218	212
a = 250, b = 3	6- to 7-year damping cycle, mean	329	291	—	—	—	—
	Equilibrium point	—	—	260	217	188	177
a = 200, b = 3	6- to 7-year damping cycle, mean	298	—	—	—	—	—
	Equilibrium point	—	267	238	194	166	150
a = 330, b = 2.5	Equilibrium point	421	371	325	274	234	227
a = 330, b = 2	Equilibrium point	535	458	391	327	264	259

[a]From starting values <40, the density of the vendace stock converges to zero.
[b]From starting values <90, the density of the vendace stock converges to zero.

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Fig. 7. Results of model simulations with constant parameter values assuming the type III functional response and the S/R relationship with $a = 330$ and $b = 3$. Densities of the vendace stock (1-year-olds and adults) for different predation scenarios: no predation on 0+ vendace, predation by brown trout only, predation by perch only, and predation by both species.

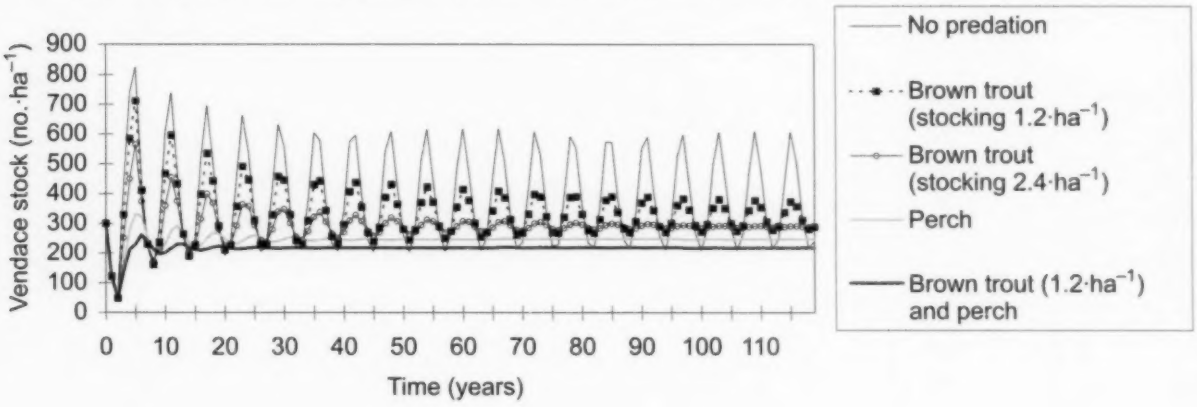
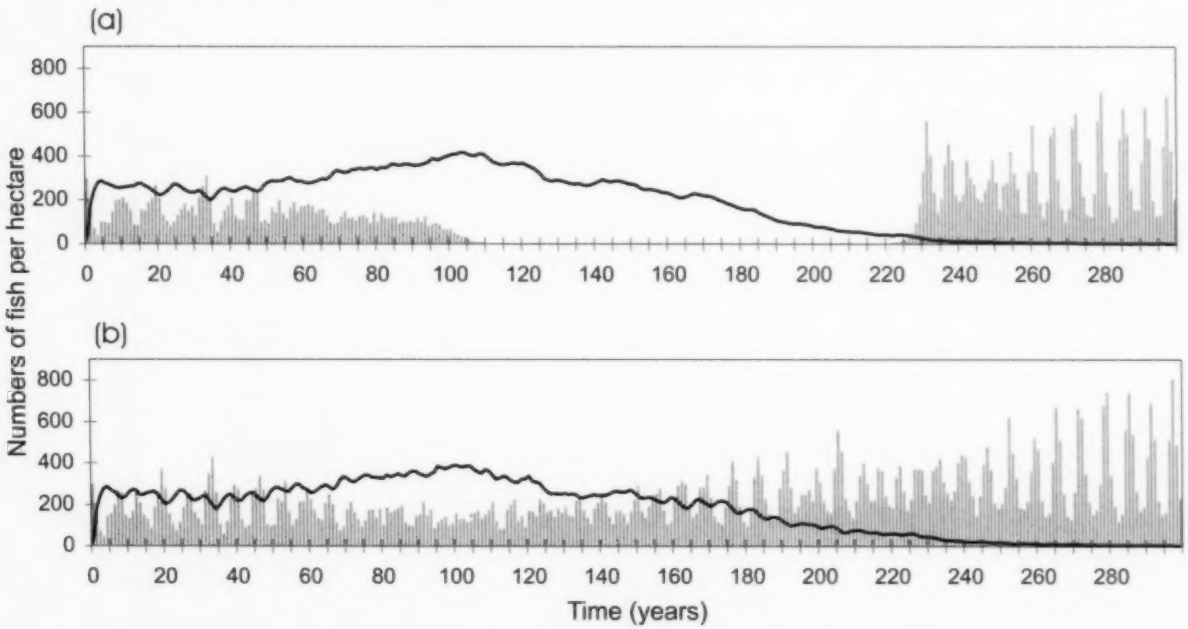


Fig. 8. Results of model simulations assuming the type II functional response in predation by brown trout and perch with the S/R relationship with $a = 330$ and $b = 3$ and random variation in three parameters. Densities of the vendace stock (bars) for two scenarios: (*a*) brown trout stocking at a density of 1.2·ha^{-1} and (*b*) no stocking with brown trout. The line is the density of pelagic perch.



lowered to a level of 200·ha^{-1}, and a more regular fluctuation with a 6- to 7-year period is established. In addition, five runs were performed with an identical random variation in perch recruitment but different randomness in the other two parameters. The pattern was very similar, which means that it was determined mainly by the density of perch. Only the timing of the collapse of the vendace differed within a range of 15 years.

The same simulation was run with no stocking of brown trout (Fig. 8*b*). In this case, the peaks in the fluctuation of the vendace are higher, no collapse occurs, and even during the high perch density, the vendace are maintained at a level of about 100·ha^{-1}.

A narrower range of variation but the same mean value for the threshold biomass in the S/R equation (3–4 kg·ha^{-1} instead of 2.5–4.5 kg·ha^{-1}) leads to a higher density level of the vendace. As a consequence, the collapse in the case of brown trout stocking does not occur until year 200 in those cases where the mortality of perch was kept constant.

Type III functional response in the predation by perch—The results of the simulations with the type III response in

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Fig. 9. Results of model simulations assuming the type III functional response in predation by perch and type II in predation by brown trout with the S/R relationship with $a = 330$ and $b = 3$ and random variation in three parameters. Densities of the vendace stock (bars) for two scenarios: (*a*) brown trout stocking at a density of 1.2·ha^{-1} and (*b*) no stocking with brown trout. The line is the density of pelagic perch.

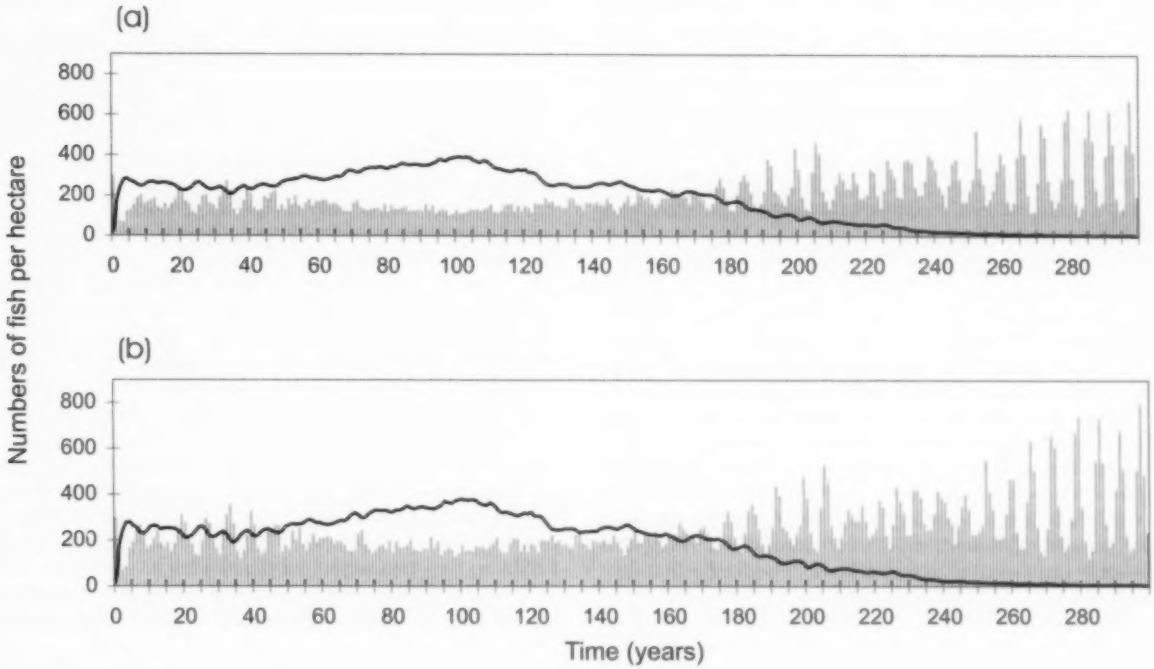
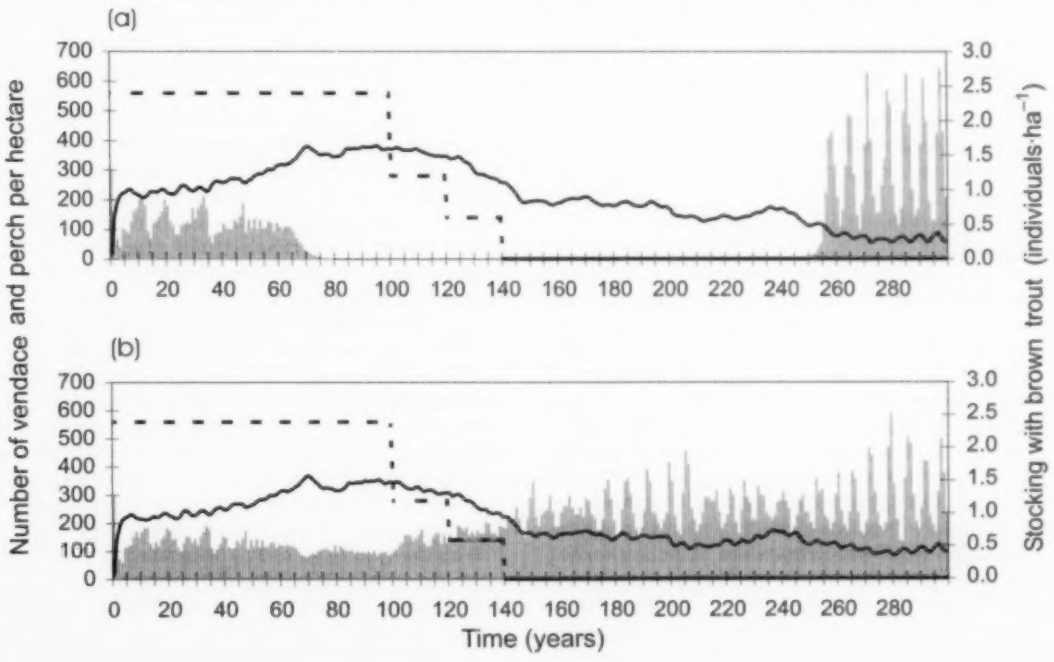


Fig. 10. Results of model simulations. Effect of decreasing stocking density of brown trout (dashed line) and perch (solid line) on the density on the vendace stock (bars) with the S/R relationship with $a = 330$ and $b = 3$ and random variation in three parameters. (*a*) Type II functional response in predation by both predators; (*b*) type III functional response for perch and type II for brown trout.



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predation by perch only and type III in predation by both predators were almost identical. In the latter case, during years 60–120, the mean and minimum densities of vendace were 14·ha^{-1} higher than in the former case, and the maximum was 15·ha^{-1} higher. Therefore, only the former case (type III response for perch only) is presented in Fig. 9. The range of fluctuation is generally narrower than with the type II response, and the vendace stock is maintained on a rather steady level during high perch density without falling to zero. The minimum densities are higher during the period of high perch density than with the type II response. With no brown trout stocking, in years 60–120, the range of fluctuation and minimum and maximum densities of vendace were 113, 128, and 241·ha^{-1}, respectively, with the type III response and 172, 76, and 248·ha^{-1}, respectively, with the type II response.

Effect of brown trout

The effect of brown trout was studied by starting the simulation with a very high stocking density (2.4·ha^{-1}) and decreasing it stepwise to zero (Fig. 10). The model was run first using the nominal S/R relationship and the type II functional response for both predators and then using the type III response for perch only. The latter run was repeated using two different S/R relationships. The random variation in the three parameters was identical in all runs. With the type II functional response, the vendace stock falls rapidly to a very low level and is not able to recover, even if the brown trout stocking was zero, until the density of perch decreases. With the type III functional response in predation by perch, the density of the vendace stock increases with the decreasing stocking density of brown trout and enters a fluctuation with a 6- to 7-year periodicity (Fig. 10*b*). The simulation results with different S/R curves were very similar to those shown in Fig. 10*b*. The lower value of a in the S/R relationship lowers the peaks in the fluctuation and the level of stock density during the period of maximum predation. Simulation with the flat S/R curve ($b = 2$) leads to a similar pattern during the high predation and similar periodic fluctuation during the latter half of the simulation period but a smaller range of fluctuation and higher mean level than with the nominal S/R curve.

Discussion

In this modelling approach, the main goal was to study the mechanisms involved in the predation processes on 0+ vendace, compare different scenarios, and consider the effect of the functional response. Because of uncertainty in many parameters, the model cannot be used to make specific predictions, but it can indicate the functions and parameters to which the system is most sensitive. In the case of vendace, it would be practically impossible to produce an accurate model simulation of an observed fluctuation over a given time period. This is because of extrinsic widely varying factors involved, such as climate, the food resources of the larvae, and changes in other fish stocks, all of which may cause large-scale irregularities in the fluctuation pattern (Viljanen 1986). Incorporating such factors into the model would hardly improve the predictions because complex models are vulnerable to misspecification and inadequate parameterization (e.g., Hilborn and Walters 1992).

There are data on vendace stocks and on the proportion of vendace in the diet of predators from different lakes. However, the use of dynamic models has been minor in vendace research. The data present a cross section of a complex dynamic system at a given time, but in the case where many simultaneous processes interact, simulating the system with a model may be the only way to examine what effects possible changes in particular variables would have in reality.

The simulations presented in this study show that predation on young-of-the-year vendace may be involved in maintaining prolonged low-density periods in vendace stocks. The results support the hypothesis presented by Auvinen (1994), Helminen and Sarvala (1994), and Valkeajärvi and Bagge (1995) that perch may play a decisive role here, even if it was most probably not the primary cause of the collapses. In contrast, the assumptions that stocking with brown trout would be significant (Helminen et al. 1997; Valkeajärvi et al. 1997; Vehanen et al. 1998) were not supported.

Here, the parameter values for brown trout are more reliable than those for perch because of a more empirical basis and the density estimates based on stocking rates. The stocking densities of brown trout in other Finnish lakes, such as Lake Oulujärvi (Vehanen et al. 1998), in the last 20 years have been at the same level (0.5–1 smolt·ha^{-1}) as in Lake Päijänne. The parameters in the functional response, however, are estimated on the basis of the data from Lake Päijänne and cannot be applied to other lakes (Heikinheimo et al. 2001).

Effect of functional response and S/R relationship

According to the modelling results, both the form of the functional response and the S/R relationship are involved in the effect of predation on the low-density dynamics of vendace stocks. The form of the functional response is crucial, especially in cases where the S/R relationship is steeply dome-shaped. In such a case, if the type II response were true for both brown trout and perch, brown trout alone would not affect the vendace stock markedly. Predation by perch alone would be able to determine the level of vendace density. However, stocking with brown trout together with strong predation by perch could cause a collapse of the vendace stock in cases where the density is depressed near to the level where the equilibrium of the system changes and converges to zero. With the type III response, the relative effect of brown trout would be larger than with the type II response. The effect of perch would be significant: it would keep the vendace stock at a very stable low level but it would not fall to zero. Brown trout would cause almost no additional effect. As a whole, the system seems to be more stable with the type III response. Further, in the third case, with the type II response in the predation by brown trout and type III in the predation by perch, perch would mainly determine the density of vendace, and brown trout would have no significant effect on the vendace stock.

With the type II functional response, a lower value of parameter a in the S/R relationship decreases the mean density level of the vendace stock and the range of fluctuation and leads more easily to a collapse of the vendace stock. A lower value of b, instead, makes the system more stable, maintain-

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ing a higher density during strong predation and decreasing the range of the fluctuation. With these rather flat S/R curves, the type of functional response is less significant, both types producing very similar simulation results, with the exception of low starting values.

The form of the functional response determines whether or not the predation can have a stabilizing effect on the prey population (Murdoch 1973; Taylor 1984). Only the type III response can principally have such an effect because it is able to cause density-dependent mortality. In any case, the stabilizing effect can occur only at low prey densities (Taylor 1984) because there is a maximum consumption limit of the predators.

In many studies dealing with the effect of predators on vendace year-class strength, the functional response was not taken into account in the calculations. The main reason for this is the lack of information on the functional response, although it is known that the predators may shift to other food species when the density of vendace is low (Jaatinen et al. 1999; Koivurinta et al. 2000) and that the predation takes a larger proportion of sparse year-classes than of dense ones (Vehanen et al. 1998; Koivurinta et al. 2000).

Considering the available data, the type II functional response seems probable in the brown trout – vendace interaction, as was assumed by Marttunen and Kylmälä (1997) and by Heikinheimo et al. (2001). The type II response may arise if the vendace juveniles are strongly favoured by the predator or easily available even at low densities compared with other alternative prey species. In Lake Puruvesi, brown trout utilized vendace as a small proportion (2–4%) in the diet, although the density of 0+ vendace was very low, nearly zero in the autumn (H. Auvinen and I. Kolari, Finnish Game and Fisheries Research Institute, Enonkoski, Finland, unpublished data). At densities of 200–300·ha^{-1} in the autumn, the 0+ vendace made up about half of the diet of brown trout and 80% at the autumn density of 1000·ha^{-1}. In the Great Lakes, the predation rates of lake trout (*Salvelinus namaycush*) were relatively consistent over a wide range of prey densities (Kitchell et al. 1994). Aggregation of the prey, for instance, at the thermocline in summer could lead to the observed pattern: effective predation even at low average prey densities in the lake (Kitchell et al. 1994).

Hildén (1988) suggested that the type III response would be more plausible in fish assemblages, as it is in vertebrate predator–prey dynamics. The type III functional response occurs mostly in connection with shifts from one prey type to another (Taylor 1984), and the most simple explanation for this type of response is that it is not profitable for the predator to hunt the prey at low densities. In the brown trout – vendace interaction, the functional response might be of type III with a very low half-saturation constant, which resembles the type II response but makes the predation mortality decrease rapidly when the prey density approaches zero. This would keep the prey stock at a steady low level during strong predation instead of converging to zero. In the case of vendace, shoaling behaviour in a sparse population probably affects the functional response curve, but this issue is still unexamined.

The type III functional response seems plausible in the predation by perch on vendace. Perch is a flexible species in its feeding habits, taking both littoral and pelagic prey (Jaatinen et al. 1999). During the sparse vendace stock (200–300·ha^{-1}) in Lake Puruvesi, perch did not feed on 0+ vendace. Smelt was the main food object of perch larger than 22 cm in the pelagic zone, but many littoral fish species and bottom animals were found in the stomachs.

Role of perch

The more decisive role of perch as a predator on young-of-the-year vendace, suggested by the simulation results, is partly due to their abundance compared with brown trout. If the density of perch were, for instance, 200 ha^{-1}, the assumed maximum consumption would be 3000 young-of-the-year vendace·ha^{-1} and that of brown trout (1 fish·ha^{-1}) only 720 vendace·ha^{-1}. In fact, the maximum consumption by perch of 0+ vendace according to Jaatinen et al. (1999) may be underestimated. According to the bioenergetics estimation by Karås and Thoresson (1992), the maximum consumption of a 100-g perch at temperatures from 15 to 20°C would be 5–10% of its weight per day, and even more for smaller perch. Thus, if one 30- to 40-g perch assumed in the model consumed 3–4 g·day^{-1}, half of which would be 0+ vendace, the biomass of vendace taken during 1 month would be 45–60 g, or 45–60 individuals, if the average weight was 1 g. On the other hand, the half-saturation constant (250) for perch in the model may be too small because the perch in Lake Puruvesi did not feed on vendace at all when the density of 0+ vendace was 200–300·ha^{-1} in the autumn. This would tend to overestimate the consumption at low densities.

The most effective feature in the perch–vendace interaction, independent of the type of functional response, is probably the behaviour of perch occupying the pelagic zone during a sparse vendace stock. The increasing predator density combined with declining vendace density leads to a depensatory effect at a range of vendace densities. The effect of perch is certainly correlated with its abundance. Large variations in perch recruitment are connected with temperature during the first spring and summer (Lehtonen and Lappalainen 1995). In Lake Päijänne, the perch density in Tehinselkä was at its highest during the years following 1988, known as a year of a warm summer and strong perch year-classes, and declined gradually during the 1990s. In Lake Pyhäjärvi, there was an abundant perch stock during the same period (Helminen et al. 1997).

The possible importance of perch was stressed by Helminen and Sarvala (1994), Auvinen (1994), and Valkeajärvi and Bagge (1995). Perch are probably not the cause of the recession in vendace stocks but may hinder the recovery of the stock. It is worth noting that in Lake Konnevesi (Valkeajärvi and Bagge 1995) and Lake Päijänne (Valkeajärvi and Salo 2000), the increase in the abundance of the perch in the pelagic zone occurred after the collapse of the vendace stock.

Because of many uncertain parameters in the model, no conclusion can be drawn about the level of perch density where the predation becomes efficient enough to maintain a low-density state in the vendace stock. This density limit can be expected to vary in different lakes. The form of the S/R curve of vendace determines the optimal spawning stock density and the highest year-class density that can be obtained. In the first place, this is connected to the fecundity of the fish and the extent and quality of the spawning and larval areas in the lake, whereas the half-saturation constant in the

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functional response determines in which range of prey densities the predation causes the highest mortality. The value of the half-saturation constant can be expected to depend on other prey species available and the prey preferences of the predator and on the presence of competing predator species.

Mechanisms behind the fluctuations of vendace stocks

There were simulations in which the model showed equilibrium points for many scenarios of vendace–predator interaction. However, irregular fluctuations with a periodic component were produced when there was random variation in some parameters.

Cyclic fluctuations in vendace stocks are thought to be caused by density-dependent processes (Viljanen 1986; Salojärvi 1987; Auvinen 1994), but there is no general agreement about how these mechanisms work. Most probably, the dominating mechanisms differ in different lakes. Salojärvi (1987) argued that the increased mortality of the vendace larvae, as a consequence of overdensity in relation to the food resources, is the most important factor in generating fluctuation and that other mechanisms such as predation or fishing tend to dampen oscillations. The hypothesis by Salojärvi (1987) is supported by the fact that dome-shaped S/R relationships have been shown for many lakes (e.g., Salojärvi 1991; Salmi and Huusko 1995), which means that moderate rather than high spawning stock densities produce the strongest year-classes. In the more productive Lake Pyhäjärvi, however, the recruitment is positively correlated with the size of the spawning stock, and density-dependent regulation in the larval stage does not seem to be strong (Helminen et al. 1997). In this case, the hypothesis of asymmetric competition between age-classes (Hamrin and Persson 1986), causing 2-year-cycles, was supported during the high-density period, but the level of recruitment was very stable during the low-density state in the 1990s (Helminen et al. 1997).

Similarly, as with predation, there is a functional response in fishing as well. The effect of fishing was not included in this study, but it is an important issue in planning the management of vendace stocks. If fishing were modelled as a constant fishing mortality, not dependent on the density of vendace, it is clear that it would not affect the basic fluctuation patterns, even if it would affect the level of stock density. Marjomäki et al. (1995) suggested a type III response in the fishery on vendace in Lake Puulavesi. Most probably there are differences between lakes. The fishermen may respond to diminishing vendace stocks by increasing their effort or by switching to new species (Sipponen et al. 1999). In Lake Päijänne, for instance, trawl fishing is continued in spite of a decline in the vendace stock because the European whitefish (*Coregonus lavaretus*) offers an alternative target for commercial fishing (Valkeajärvi and Salo 2000). To predict the effect of fishing on the vendace stocks, more should be known about the functional response. Salojärvi (1987) assumed that fishing would have a stabilizing effect, but as seen in the case of predation, this may not be true in all cases.

In conclusion, the dynamic modelling approach gave new insight into the problem of interspecies interactions involved in the low-density dynamics of vendace stocks. Compared with the studies based on equilibrium assumptions, even contradictory conclusions were obtained. The importance of modelling in the research on the complex dynamics of fish stocks is emphasized. The results revealed that the type of functional response is decisive in assessing the effect of predation on a prey stock with a steep dome-shaped relationship between spawning stock and recruitment, and the same is expected to concern the effect of fishing as well. These issues are crucial in the management of vendace stocks and in evaluating the effects of stocking of predator fish into vendace lakes. More attention should be paid to these problems in future research.

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Fish-mediated nutrient recycling and the trophic cascade in lakes

José Luiz Attayde and Lars-Anders Hansson

Abstract: The effects of planktivorous fish on phytoplankton through nutrient recycling and zooplankton herbivory were experimentally separated and their relative importance quantified in a eutrophic humic lake. Natural phytoplankton assemblages were incubated in nutrient-permeable chambers placed inside enclosures with or without fish. Outside these chambers, phytoplankton were exposed to zooplankton herbivory and to nutrient recycling by fish and zooplankton, whereas inside the chambers, phytoplankton were exposed only to nutrient recycling by these consumers. Our results show that fish had significant positive effects on cyanobacteria, cryptomonads, and chlorophytes inside the chambers, indicating that fish-mediated nutrient recycling had significant effects on these phytoplankton groups. However, our results also indicate that changes in zooplankton grazing induced by fish were an important mechanism by which fish affected all phytoplankton groups except cyanobacteria. Comparison of effect sizes revealed that the effects on cyanobacteria and chlorophytes through nutrient recycling were stronger than those through zooplankton grazing. Moreover, most of the fish-mediated nutrient recycling effects were due to increased nutrient recycling by zooplankton rather than direct nutrient excretion by fish. In conclusion, we provide experimental evidence supporting the hypothesis that fish-mediated nutrient recycling is an important mechanism affecting phytoplankton community structure and favoring cyanobacteria dominance in lakes.

Résumé : Les effets des poissons planctonophages sur le phytoplancton par le biais du recyclage des éléments nutritifs et l'herbivorie du zooplancton ont pu être séparés expérimentalement et leurs importances relatives quantifiées dans un lac humique eutrophe. Des peuplements naturels de phytoplancton ont été mis en incubation dans des contenants perméables aux nutriments placés dans des enceintes avec ou sans poissons. À l'extérieur des contenants, le phytoplancton était exposé à l'herbivorie du zooplancton et au recyclage des éléments nutritifs par le zooplancton et les poissons, alors que, dans les contenants, le phytoplancton était exposé seulement au recyclage des nutriments par ces consommateurs. Nos résultats indiquent que les poissons ont des effets positifs sur les cyanobactéries, les cryptomonadines et les chlorophytes à l'intérieur des contenants, ce qui montre que le recyclage des nutriments généré par les poissons a des effets significatifs sur ces groupes phytoplanctoniques. Cependant, nos résultats indiquent aussi que le broutage du zooplancton sous l'effet des poissons est un mécanisme significatif par lequel les poissons affectent les groupes phytoplanctoniques, à l'exception des cyanobactéries. Une comparaison des importances relatives des effets montre que les conséquences sur les cyanobactéries et les chlorophytes du recyclage des nutriments sont plus grandes que celles du broutage du zooplancton. De plus, la plupart des effets dus au recyclage des éléments par l'action des poissons sont occasionnés par un recyclage accru des nutriments par le zooplancton, plutôt que par une excrétion directe de nutriments par les poissons. En conclusion, on trouve ici des preuves expérimentales que le recyclage des nutriments par l'action des poissons est un mécanisme important qui affecte la structure de la communauté phytoplanctonique et qui favorise la dominance des cyanobactéries dans les lacs.

[Traduit par la Rédaction]

Introduction

It has been well demonstrated in lakes that planktivorous fish selectively consume large zooplankton, shift zooplankton communities toward dominance by smaller species or individuals (reviewed by Gliwicz and Pijanowska 1989), increase phytoplankton biomass and productivity (Carpenter and Kitchell 1993), and often change phytoplankton communities toward dominance by cyanobacteria (e.g., Reinertsen et al. 1986; Starling and Rocha 1990; Vanni and Findlay 1990). Several enclosure and whole-lake experiments have shown that reduced stocks of planktivorous fish may cause decreases in both algal biomass and dominance of cyanobacteria (e.g., Reinertsen et al. 1990; Vanni and Findlay 1990), and many attempts have been made to improve the water quality of eutrophic lakes through removal of fish (e.g., Gulati et al. 1990; Hansson et al. 1998; Hansson and Bergman 1999). Although the effects of planktivorous fish on phytoplankton have been well demonstrated, the relative importance of the mechanisms accounting for these effects are still not clear.

Several previous studies have shown that large-bodied zooplankton generally have higher mass-specific grazing rates

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than small zooplankton and can effectively graze a broader range of size-classes and morphologies of phytoplankton (reviewed by Sterner 1989). Therefore, planktivorous fish can reduce zooplankton grazing on phytoplankton by decreasing zooplankton size structure, and this can potentially explain the positive response of phytoplankton to fish. However, several enclosure and whole-lake experiments have demonstrated that the effects of planktivorous fish on phytoplankton cannot be explained by variations in zooplankton grazing alone (Vanni and Findlay 1990; Schindler 1992; Vanni and Layne 1997). Moreover, colonial or filamentous cyanobacteria are highly resistant to zooplankton grazing, and there is reason to doubt that their positive response to planktivorous fish is due to reduced zooplankton grazing.

By changing zooplankton species composition and size structure, planktivorous fish can also affect the rates and ratios by which zooplankton recycle nutrients to phytoplankton. Because small-bodied zooplankton have higher mass-specific rates of nutrient recycling than large zooplankton (reviewed by Sterner 1989), an assemblage dominated by small zooplankton should recycle nutrients at higher rates than an assemblage of equal biomass dominated by large zooplankton (Carpenter and Kitchell 1993). Therefore, planktivorous fish may indirectly increase nutrient recycling rates by zooplankton, if total zooplankton biomass is not reduced by fish (Ramcharan et al. 1996). Moreover, large cladocerans like *Daphnia* have higher P and lower N demand than smaller cladocerans and copepods and may release nutrients at higher N:P ratios (Sterner et al. 1992; Sterner and Hessen 1994). Because the N:P supply ratio can have strong effects on phytoplankton community structure and dynamics (reviewed by Sommer 1989), shifts in this ratio driven by fish may have important effects on phytoplankton communities (Attayde and Hansson 1999). In particular, fish might decrease the N:P ratio released by zooplankton (Sterner et al. 1992) and thereby favor cyanobacteria, which have a strong competitive advantage under low N:P ratios (Smith 1983).

Planktivorous fish can also affect phytoplankton communities by directly releasing nutrients through excretion and defecation (Vanni and Findlay 1990; Schindler 1992; Vanni and Layne 1997). Nutrient excretion by fish has long been considered an important source of nutrients to phytoplankton (Lamarra 1975), and some studies have shown that fish can recycle nutrients at rates exceeding external nutrient loading rates (Braband et al. 1990; Reinertsen et al. 1990; Persson 1997). Since fish release nutrients at low N:P ratios (Braband et al. 1990; Schindler and Eby 1997; Attayde and Hansson 1999), they might also favor cyanobacteria directly by their own waste products. In addition, the pulsed release of nutrients from fish contrary to zooplankton may favor the uptake kinetics of cyanobacteria (Reinertsen et al. 1986).

Hence, planktivorous fish can affect the structure and dynamics of phytoplankton communities through both zooplankton grazing and nutrient recycling mechanisms. However, the extent to which different algal groups respond to fish-mediated nutrient recycling effects and whether these effects are more important than those through zooplankton herbivory is unclear. Here, we present results of a press perturbation experiment in a Swedish lake designed to examine the relative importance of these mechanisms. Our approach was to measure the effect size of fish on the net changes in algal biovolume during the experiment. With such an approach, the relative importance of each mechanism was ascertained by comparing the magnitude of one effect relative to that of the other. We demonstrate that fish effects on cyanobacteria and chlorophytes through nutrient recycling can actually be more important than those through zooplankton grazing. Our results also suggest that most of the fish-mediated nutrient recycling effects were due to fish-induced effects on nutrient recycling by zooplankton.

Material and methods

Study site

The experiment was conducted in Dagstorpssjön, a eutrophic and humic lake situated in the middle of Scania, southern Sweden. The lake area is 0.48 km^2, maximum depth is 5 m, and mean depth is 2.8 m. Perch (*Perca fluviatilis*) is the most important species of fish in the lake and can have strong effects on zooplankton and phytoplankton dynamics (Romare et al. 1999). During our experiment, the concentrations of chlorophyll *a* and total P in the lake ranged from 29 to 77 $\mu g \cdot L^{-1}$ and from 39 to 47 $\mu g \cdot L^{-1}$, respectively, while the dissolved organic C concentration ranged from 8.78 to 9.54 $mg \cdot L^{-1}$. At the start of the experiment, the phytoplankton community in the lake was dominated by cyanobacteria, while rotifers dominated the zooplankton community.

Experimental design

The experiment was conducted from August 12 to September 10, 1997. Two treatments were employed with four replicates: a control treatment containing natural plankton densities with no addition of fish and a fish treatment containing natural plankton densities plus three perch (*P. fluviatilis*) about 8 cm long. Inside each enclosure, we placed nutrient-permeable chambers of approximately 0.63 m^3 (made of a 10-μm-mesh net) where natural phytoplankton assemblages were incubated, after screening 300 L of lake water through a 100-μm-mesh net to remove large zooplankton. Inside these chambers, phytoplankton were exposed to nutrient recycling by zooplankton and fish but not to herbivory from zooplankton larger than 100 μm, while outside the chambers, phytoplankton were exposed to both zooplankton herbivory and nutrient recycling by these consumers. This experimental design is similar to the design of Vanni and Layne (1997), but our chambers had a mesh size twice as large and held a volume 10 times greater than the chambers used by Vanni and Layne (1997). Because the chambers allowed phytoplankton cells smaller than 10 μm to pass through and because the filtration before incubation removed algae larger than 100 μm, we only include the response of taxa with greatest axial linear dimension larger than 10 μm and smaller than 100 μm in our estimates of phytoplankton response to fish.

Enclosures were made of thin, clear polyethylene formed into a cylindrical tube and suspended from a wooden frame buoyed by styrofoam floats. Enclosures were sealed at the bottom and open to the atmosphere at the top. The diameter of the enclosures was 1.6 m and the depth was 1.5 m, yielding a volume of approximately 3 m^3. The diameter of the chambers was 0.4 m and the depth was 0.5 m, yielding a volume of approximately 0.63 m^3. Twice a week, the enclosures and the chambers were brushed to avoid colonization by periphyton on the walls and carefully checked for dead fish, since decaying fish could affect the outcome of the experiment (Threlkeld 1987). No fish died during the experiment.

The fish stocking rate used in our experiment (about 70 $kg \cdot ha^{-1}$) was a reasonable amount of fish for a lake with total P concentrations of aproximately 40–50 $\mu g \cdot L^{-1}$ (Hanson and Leggett 1982).

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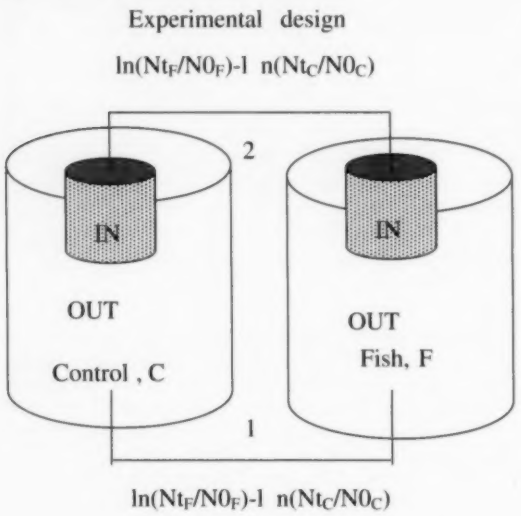
Fig. 1. Schematic representation of the experimental design and the mechanisms assessed in this study.



- 1) Total effect of fish
- 2) Fish effect through nutrient recycling from both zooplankton and fish
- 1- 2 = Fish effect through zooplankton herbivory

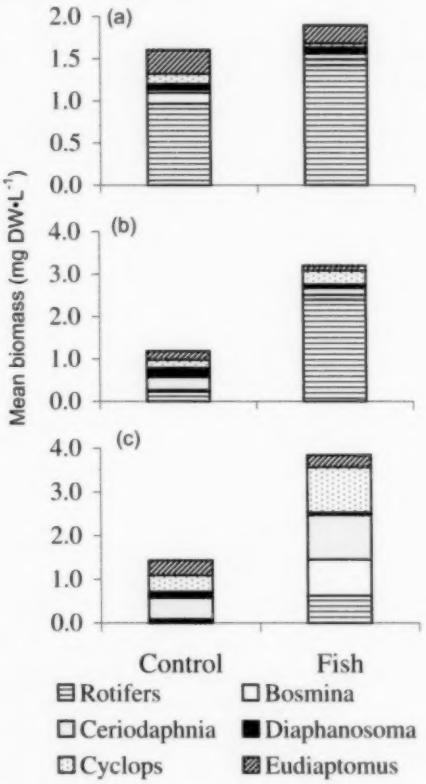
Fish were also fed with 3 g (wet weight) of chironomid larvae every 3 days and the same amount of chironomids was added to the control to avoid biased enrichment of the fish treatment. This amount of chironomids constituted a ration size of approximately 2% of the fish weight per day. We added chironomids because many planktivorous fishes under natural conditions, including the 1+ perch used in our experiment, also eat benthic prey and excrete nutrients from benthic habitats into pelagic habitats, which may have important consequences for planktonic communities (Schindler et al. 1996; Vanni 1996; Schaus and Vanni 2000).

Sampling and counting

Phytoplankton samples were collected at the beginning, middle, and end of the experiment (days 1, 14, and 28, respectively) from both outside and inside the chambers of each enclosure and were preserved with acid Lugol's solution. Algae were counted at 250× magnification on permanent slides made using HPMA (Crumpton 1987). In each sample, a minimum of 10 fields or 200 cells were counted. The length and width of 20 individuals of each algal species were measured and the biovolumes were calculated using different formulae according to their geometric shape (Tikkanen and Willén 1992).

Zooplankton samples were also taken from outside the chambers, filtered through a 10-μm-mesh net to concentrate the organisms, and preserved with acid Lugol's solution. Organisms were counted at 100× magnification with an inverted microscope, after sedimentation in 10-mL chambers for at least 2 h. At least 200 organisms of each group were counted per zooplankton sample. For each zooplankton sample, the length of 20 individuals of each taxon was measured and the respective biomass calculated using specific length–weight regression equations reported in Dumont et al. (1975) and Bottrell et al. (1976). The biomass of each taxon in a given sample was estimated as the product of its mean biomass and density in that sample. Total zooplankton biomass was estimated as the sum of the total biomass of rotifers, cladocerans, and copepods.

Fig. 2. Mean biomass of total zooplankton and the relative importance of rotifers, cladocerans, and copepods in the fish and control treatments after (*a*) 1 day, (*b*) 14 days, and (*c*) 28 days from the start of the experiment.



Data analysis

The total effect of fish on phytoplankton was assessed as the difference between the net changes in algal biovolume outside the chambers of the fish and control treatments (Fig. 1). The effect of fish on phytoplankton through nutrient recycling was assessed as the difference between the net changes in algal biovolume inside the chambers of the fish and control treatments (Fig. 1). The difference between the fish effects outside and inside the chambers was used as an estimate of the fish effect on phytoplankton through zooplankton grazing (Fig. 1). Hence, the magnitude of the fish effect on phytoplankton outside or inside the chambers was estimated as $\ln(N_{t,F}/N_{0,F}) - \ln(N_{t,C}/N_{0,C})$ where t is the duration of the experiment (14 or 28 days) and $N_{t,F}$ and $N_{t,C}$ (or $N_{0,F}$ and $N_{0,C}$) are the algal biovolume at t days (or at the start) of the experiment in the fish and control treatments, respectively (modified from Osenberg et al. 1997). The ratios of abundances (N_t/N_0) were log transformed before the effect size metric was calculated to stabilize variances in the effect size data as well as provide a symmetrical scale. In order to express the full range of variation in our experiment, the effect of fish outside or inside the chambers was calculated for each replicate of the fish treatment as the change relative

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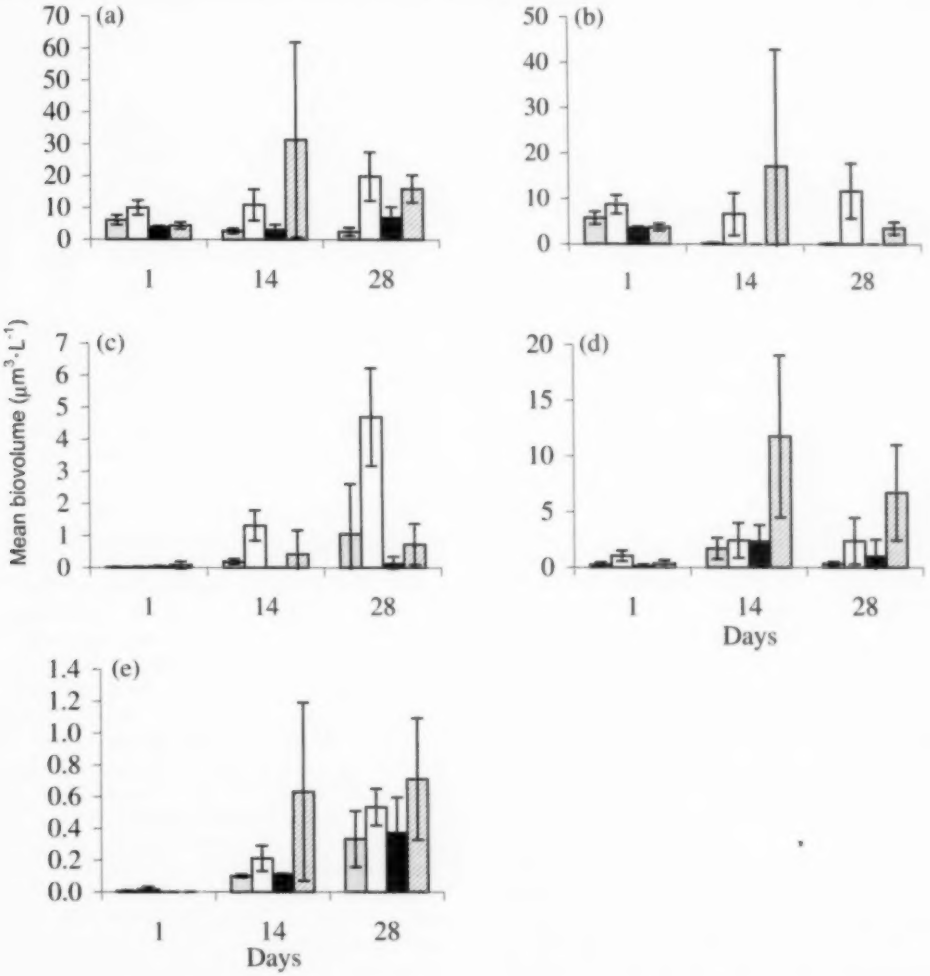
Fig. 3. Mean (±1 SD) biovolume of (*a*) total phytoplankton, (*b*) cyanobacteria, (*c*) cryptomonads, (*d*) diatoms, and (*e*) chlorophytes outside and inside the chambers of the fish and control treatments after 1, 14, and 28 days from the start of the experiment. Control out, grey bars; fish out, open bars; control in, solid bars; fish in, hatched bars.



to each control replicate (4 × 4 replicates = 16 effect size estimates). From these distributions of effect size, we calculated the mean and standard deviation of each fish effect.

A *t* test was used to test for differences between treatment effects on the net changes in algal biovolume. A significant difference between the changes in algal biovolume outside the chambers of the fish and control treatments indicates that the total effect of fish was significantly different from zero ($\ln(N_{t,F}/N_{0,F}) - \ln(N_{t,C}/N_{0,C}) \neq 0$). Likewise, a significant difference between the changes in algal biovolume inside the chambers of the fish and control treatments indicates that the effect of fish through nutrient recycling mechanisms was significantly different from zero. A paired-sample *t* test was used to test for differences between the fish effects on phytoplankton outside and inside the chambers. Here, the null hypothesis was that the effects of fish through nutrient recycling (inside) were not significantly different from the total effect of fish (outside). Since statistical significance does not measure the biological importance of a factor or mechanism, the relative importance of the fish effects through zooplankton herbivory and nutrient recycling mechanisms was ascertained by comparing the effect size of one factor relative to that of the other.

Table 1. Mean and SD of total zooplankton biomass in the control (C) and fish (F) treatments after 1, 14, and 28 days from the start of the experiment.

Days	Mean C	SD C	Mean F	SD F
1	1.64	0.38	1.91	0.14
14	1.28	0.23	3.28	1.72
28	1.51	1.16	3.96	0.49

Results

At the start of the experiment, the zooplankton community was dominated by rotifers (Fig. 2), while the phytoplankton community was dominated by cyanobacteria in

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Table 2. Mean and SD of the net change in biovolume of the major taxonomic groups inside and outside the chambers of the control (C) and fish (F) treatments after 14 and 28 days from the start of the experiment and results of the t test (df = 6) for differences between treatment effects on algal biovolume changes.

	Inside						Outside					
	Mean C	SD C	Mean F	SD F	t	p	Mean C	SD C	Mean F	SD F	t	p
Day 14												
Total algae	–0.39	0.75	1.52	1.10	–2.88	0.01	–0.82	0.39	0.04	0.60	–2.41	0.03
Cryptomonads	–0.16	0.13	0.27	1.71	–0.49	0.32	0.80	0.67	2.44	0.38	–4.24	<0.01
Cyanobacteria	–3.59	0.07	0.24	2.09	–3.66	0.01	–3.39	0.72	–0.48	0.82	–5.31	<0.01
Chlorophytes	0.68	0.39	1.63	1.02	–1.75	0.07	0.60	0.42	0.87	0.61	–0.73	0.25
Diatoms	1.98	1.59	3.23	0.84	–1.40	0.11	1.60	0.96	0.67	1.16	1.23	0.13
Day 28												
Total algae	0.47	0.61	1.29	0.30	–2.40	0.03	–0.99	0.61	0.66	0.28	–4.92	<0.01
Cryptomonads	0.30	0.66	1.43	1.17	–1.68	0.07	1.54	1.56	3.68	0.28	–2.71	0.02
Cyanobacteria	–3.57	0.06	–0.09	0.40	–17.17	<0.01	–3.52	0.79	0.21	0.38	–8.51	<0.01
Chlorophytes	1.44	0.58	2.00	0.51	–1.46	0.10	1.34	0.41	1.69	0.28	–1.40	0.10
Diatoms	0.76	1.96	2.45	1.28	–1.44	0.10	0.29	0.83	0.49	1.28	–0.26	0.40

both treatments (Fig. 3). During the experiment, the total biomass of zooplankton doubled in the fish treatment but remained approximately constant in the control (Fig. 2; Table 1). Fish significantly increased total zooplankton biomass after both 14 days ($t = 2.30$, $p = 0.05$) and 28 days ($t = 3.89$, $p < 0.01$), and this was mainly due to an increase in rotifer biomass after 14 days and an increase in *Bosmina*, *Ceriodaphnia*, and *Cyclops* biomass after 28 days (Fig. 2). The total biovolume of phytoplankton also increased both outside and inside the chambers of the fish treatment but slightly decreased outside the chambers of the control (Fig. 3). The increase in total algal biovolume in the presence of fish was mainly due to an increase in the biovolumes of cyanobacteria, diatoms, and cryptomonads, while the decrease in total algal biovolume in the control was mainly due to a disapearance of cyanobacteria in the absence of fish (Fig. 3).

Outside the chambers, where phytoplankton were exposed to grazing by zooplankton and to nutrient recycling by fish and zooplankton, the biovolume of cryptomonads increased in both treatments ($\ln(N_t/N_0)$ was positive), but this increase was significantly higher in the fish treatment than in the control (Table 2). On the other hand, the biovolume of cyanobacteria decreased in both treatments after 14 days ($\ln(N_t/N_0)$ was negative), but this decrease was significantly lower in the fish treatment than in the control (Table 2). Significant positive effects of fish on cyanobacteria were also found after 28 days of experiment (Table 2). Fish also had significant effects on total phytoplankton biovolume during the experiment (Table 2).

Inside the chambers, where phytoplankton were exposed to nutrient recycling by zooplankton and fish but not to grazing by zooplankton larger than 100 μm, fish had significant effects on total phytoplankton biovolume as well as on the biovolumes of cyanobacteria, chlorophytes, and cryptomonads (Table 2). This clearly indicates that fish had effects on phytoplankton independent of their effects on zooplankton grazing. Furthermore, examining the response of the major phytoplankton genera to fish reveals that fish had significant effects on the biovolume of *Microcystis*, *Scenedesmus*, and *Snowella* both outside and inside the chambers (Table 3), indicating that part of their response to fish outside the chambers was actually due to nutrient recycling mechanisms mediated by fish.

Quantifying the magnitude of these fish effects reveals that cyanobacteria had the strongest positive response to fish both outside and inside the chambers. Results of the paired t test show that these responses were not significantly different from each other (Table 4), suggesting that fish effects on cyanobacteria were mainly through nutrient recycling mechanisms. In addition, we found no differences between the fish effects on chlorophytes outside and inside the chambers at the end of the experiment (Table 4), suggesting that fish-mediated nutrient recycling can also account for most of the fish effects on chlorophytes. However, the relative importance of the fish effects through nutrient recycling (inside the chambers) and zooplankton herbivory (outside minus inside the chambers) was assessed by comparing the effect size of one mechanism relative to that of the other. Indeed, this comparison indicates that the effects of fish on cyanobacteria and chlorophytes through nutrient recycling were stronger than those through zooplankton herbivory (Table 4). On the other hand, the effects of fish on cryptomonads and diatoms through zooplankton herbivory were stronger than those through nutrient recycling after 14 days but not after 28 days of experimentation (Table 4). After 14 days, fish had stronger effect on total phytoplankton through nutrient recycling, but at the end of the experiment, this effect was of similar magnitude to that through zooplankton grazing (Table 4).

Finally, the effect size estimates show that fish had positive effects on all phytoplankton groups (except diatoms after 14 days) both outside and inside the chambers (Table 4). However, the effects of fish on cryptomonads were stronger outside than inside the chambers, while those on chlorophytes and diatoms were stronger inside than outside the chambers (Table 4). This suggests that fish had positive effects on cryptomonads but negative effects on chlorophytes and diatoms through zooplankton grazing (outside minus inside, Table 4). Results also suggest that the effects of fish on cyanobacteria and total phytoplankton through zooplankton grazing (outside minus inside) were negative after 14 days but positive after 28 days (Table 4).

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Table 3. Mean and SD of the net change in biovolume of the major taxa inside and outside the chambers of the control (C) and fish (F) treatments after 14 and 28 days from the start of the experiment and results of the *t* test (df = 6) for differences between treatment effects on algal biovolume changes.

Inside							Outside						
	Mean C	SD C	Mean F	SD F	*t*	*p*		Mean C	SD C	Mean F	SD F	*t*	*p*
Day 14							Day 14						
Cosmarium	0.23	0.45	0.84	0.54	–1.74	0.07	Green colony	0.02	0.10	0.35	0.29	–2.17	0.04
Microcystis	0.00	0.00	2.63	3.08	–1.71	0.07	*Microcystis*	0.00	0.00	2.20	2.57	–1.71	0.07
							Scenedesmus	0.07	0.05	0.41	0.30	–2.21	0.03
Snowella	–2.80	0.21	0.33	1.45	–4.29	<0.01	*Snowella*	–2.90	0.84	–1.60	1.42	–1.57	0.08
Day 28							Day 28						
Cosmarium	0.58	0.49	1.34	0.53	–2.09	0.04	Green colony	0.04	0.08	0.36	0.17	–3.50	0.01
Microcystis	0.00	0.00	3.45	0.34	–20.47	<0.01	*Microcystis*	0.00	0.00	3.72	1.23	–6.02	<0.01
Scenedesmus	0.16	0.18	0.43	0.24	–1.82	0.06	*Scenedesmus*	0.11	0.03	0.92	0.81	–2.01	0.05
Snowella	–2.80	0.21	–1.84	0.82	–2.27	0.03	*Snowella*	–3.04	0.81	–1.30	0.45	–3.75	<0.01

Note: Only taxa showing significant differences (at the 10% level) are shown.

Discussion

It has been demonstrated repeatedly in lakes that planktivorous fish can have strong effects on the structure and dynamics of planktonic communities (reviewed by Lazzaro 1987). However, the relative importance of the different mechanisms accounting for the effects of fish on phytoplankton is still not clear. It is also unknown which phytoplankton groups exhibit the largest response to nutrient recycling effects mediated by fish. In the present study, we have demonstrated that fish can actually have effects on cyanobacteria and chlorophytes through nutrient recycling that are stronger than their effects through zooplankton grazing. To our knowledge, only two previous studies have experimentally separated and quantified the effects of fish through nutrient recycling on the structure and dynamics of phytoplankton communities (Schindler 1992; Vanni and Layne 1997). Schindler (1992) concluded that nutrient excretion by fish explained most of the fish effects on total algal biomass and suggested that changes in zooplankton grazing were not a very important mechanism by which fish affected phytoplankton. Vanni and Layne (1997) also found that fish had substantial effects on phytoplankton through nutrient recycling, but it is not clear from their results if these effects were more important than those through zooplankton grazing.

Our study suggests that fish-mediated nutrient recycling may account for most of the total phytoplankton response to fish when the phytoplankton community is dominated by cyanobacteria or chlorophytes. This result has important implications for lake management because most attempts to improve the water quality of eutrophic lakes through biomanipulation have been based on the idea that reduced stock of planktivorous fish should lead to increased zooplankton grazing on phytoplankton and thereby reduced phytoplankton biomass and increased water transparency. However, as the phytoplankton communities of eutrophic lakes are often dominated by cyanobacteria and chlorophytes, planktivorous fish removal should affect total phytoplankton biomass mainly through nutrient recycling mechanisms in such lakes.

Obviously, the fact that fish can influence phytoplankton by altering nutrient recycling does not imply that fish-induced changes in zooplankton grazing cannot have important effects on phytoplankton communities. Many studies have shown that zooplankton grazing has strong effects on phytoplankton communities (reviewed by Sterner 1989), and our study also indicates that fish-induced changes in zooplankton grazing had significant effects on all phytoplankton groups except cyanobacteria. Our results show that the effects of fish through nutrient recycling (inside the chambers) were significantly different from the total effect of fish (outside the chambers), suggesting that alterations of zooplankton grazing was an important mechanism by which fish affected phytoplankton.

In our study, we have not separated the two mechanisms by which fish can affect phytoplankton through nutrient recycling: by directly releasing nutrients and by changing the rates and ratios at which zooplankton release nutrients (Vanni and Findlay 1990; Schindler 1992; Vanni and Layne 1997). The only study that has experimentally separated

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Table 4. Mean effect size and SD of the fish effects on algal biovolume outside (OUT) and inside (IN) the chambers excluding mesozooplankton, the difference between the mean effect sizes outside and inside the chambers (OUT – IN), and results of the paired *t* test (df = 15) for significant differences between these fish effects.

	Mean OUT	SD OUT	Mean IN	SD IN	Mean OUT – IN	*t* test *p*
Day 14						
Total algae	0.86	0.64	1.91	1.19	–1.05	<0.01
Cryptomonads	1.64	0.69	0.42	1.53	1.21	<0.01
Cyanobacteria	2.91	0.98	3.83	1.87	–0.92	0.14
Chlorophytes	0.27	0.66	0.95	0.97	–0.68	<0.01
Diatoms	–0.93	1.35	1.26	1.61	–2.18	<0.01
Day 28						
Total algae	1.66	0.60	0.82	0.61	0.84	<0.01
Cryptomonads	2.14	1.42	1.13	1.20	1.01	0.01
Cyanobacteria	3.73	0.78	3.48	0.36	0.25	0.31
Chlorophytes	0.35	0.44	0.56	0.69	–0.21	0.43
Diatoms	0.20	1.36	1.69	2.10	–1.49	0.02

these two mechanisms suggested that nutrient recycling by fish can have stronger effects on phytoplankton communities than nutrient recycling by zooplankton (Vanni and Layne 1997). However, the relative importance of nutrient recycling by fish and zooplankton depends, among other things, on their relative biomass (Schindler et al. 1996).

Although we did not measure nutrient recycling rates in our experiment, our results suggest that increased zooplankton excretion was probably more important than direct excretion by fish because zooplankton biomass was higher than the fish biomass in the fish treatment. The biomass of fish stocked in our 3-m^3 enclosures was approximately 6 g dry weight, while the total biomass of zooplankton was about 9–12 g dry weight in the enclosures with fish and 3–4.5 g dry weight in the enclosures without fish. As expected from body size differences, zooplankton have a higher nutrient release rate per unit of biomass than fish, and we have shown in a previous study (Attayde and Hansson 1999) that the mass-specific nutrient release rates of zooplankton (*Daphnia magna*) are about 10 times those of 1+ fish (*Rutilus rutilus*). Therefore, increased nutrient excretion by zooplankton might have accounted for most of the fish-mediated nutrient recycling effects on phytoplankton in our experiment.

Finally, it should be noted that most studies that have investigated the effects of planktivorous fish on phytoplankton and zooplankton communities have been conducted in enclosures that were isolated from the sediment. However, many planktivorous fish, including our fish species *P. fluviatilis*, can feed on benthic/littoral resources and excrete nutrients in the pelagic zone, providing a net source of "new" nutrients to phytoplankton (Schindler et al. 1996; Vanni 1996; Schaus and Vanni 2000). Although our enclosures were also closed to the sediment, fish were fed benthic prey (chironomids) and thereby stimulated phytoplankton by releasing "new" nutrients into the enclosures. In doing so, fish may indirectly benefit zooplankton above and beyond any potential negative effects of their zooplanktivory (Attayde and Hansson 2001). Indeed, in our study, total zooplankton biomass increased in the presence of fish, partly due to this positive indirect effect of fish excretion but also due to a compensatory increase in small zooplankton biomass following reduction of larger competitively superior zooplankton.

By increasing total zooplankton biomass, planktivorous fish might have a positive effect on phytoplankton by increasing zooplankton nutrient recycling but also a negative effect by increasing zooplankton grazing. Conversely, the opposite effects would be expected when planktivorous fish reduce total zooplankton biomass (Ramcharan et al. 1996). Therefore, how phytoplankton will respond to fish should depend on the relative strength of the different mechanisms by which fish can affect phytoplankton and on how total zooplankton biomass responds to fish.

In conclusion, we have provided experimental evidence supporting the hypothesis that fish-mediated nutrient recycling has important effects on phytoplankton community structure. In particular, we have demonstrated that most of the positive effects of planktivorous fish on cyanobacteria and chlorophytes were due to nutrient recycling effects mediated by fish, most likely due to increased nutrient recycling by zooplankton in the presence of fish. The strength and direction of the phytoplankton response to fish are highly variable, and a major challenge to aquatic food web ecologists is understanding why this response is so variable (Brett and Goldman 1996). By quantifying the relative importance of the different mechanisms by which fish can affect phytoplankton under different environmental conditions, aquatic ecologists would better understand and predict the phytoplankton response to fish.

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Successful recovery of the physiological status of coho salmon on board a commercial gillnet vessel by means of a newly designed revival box

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Abstract: Successful application of fish-revival techniques in commercial fishing prior to release of nontarget species requires clear evidence that recovery devices do indeed improve physiological status and minimize postcapture delayed mortality. This study provides such evidence for a newly designed recovery box (Fraser box) that assisted gill ventilation. Immediately after capture by gillnet, adult coho salmon (*Oncorhynchus kisutch*) were in a state of severe metabolic exhaustion and stress, based on a comprehensive analysis of plasma and muscle tissue. However, when placed in a Fraser recovery box for 1–2 h, both lethargic and vigorous fish showed significant metabolic recovery and their ability to swim was also quickly restored. An emphatic demonstration of the benefit of the Fraser box was the successful revival of >90% of fish that appeared dead at capture. Furthermore, postcapture delayed mortality was only 2.3% after a 24-h observation period. Therefore, in the context of commercial salmon gillnet fishing, revival of nontarget coho salmon in a Fraser box, in combination with a soak time (total time the gillnet is in the water) ≤70 min and careful fish handling to minimize physical trauma, could improve physiological status, restore swimming ability, and markedly reduce postcapture delayed mortality.

Résumé : Pour que l'application de techniques de réanimation de poissons non-ciblés avant leur rejet à l'eau lors de pêches commerciales soit un succès, il faut s'assurer que les moyens de rétablissement améliorent de fait la condition physiologique et minimisent la mortalité différée après la capture. Notre étude fournit une telle assurance dans le cas de l'utilisation d'une enceinte de rétablissement récemment conçue (la boîte de Fraser) qui favorise la ventilation des branchies. Immédiatement après leur capture au filet maillant, les Saumons coho adultes (*Oncorhynchus kisutch*) sont en état d'épuisement métabolique et de stress, comme l'indique une analyse détaillée du plasma et du tissu musculaire. Cependant, après 1–2 h dans la boîte de rétablissement de Fraser, tant les poissons léthargiques que les poissons vigoureux font preuve d'un rétablissement métabolique significatif et retrouvent rapidement leur capacité de nage. Une démonstration significative de l'efficacité de la boîte de Fraser est que plus de 90 % des poissons qui semblaient morts à la capture s'y sont rétablis avec succès. De plus, la mortalité différée après la capture était de seulement 2,3 % après une période d'observation de 24 h. Dans le cas de la pêche commerciale au saumon à l'aide de filets maillants, la réanimation des Saumons coho non ciblés par la pêche, combinée à un temps de mouillage des filets de ≤70 min et une manutention soignée des poissons de façon à minimiser les traumatismes physiques, peut donc améliorer la condition physiologique, rétablir la capacité de nage et réduire de façon marquée la mortalité différée.

[Traduit par la Rédaction]

Introduction

With certain stocks of Pacific coho salmon (*Oncorhynchus kisutch*) reduced to alarmingly low levels, coho salmon captured as by-catch in commercial and recreational fisheries represent an unnecessary potential loss to threatened fish stocks. If nontarget fish are discarded after capture, i.e., thrown back with no attempt at revival, they may have a low chance of survival. Estimates of postcapture delayed mortality in commercial fishing or recreational angling range from 0 to 75%, depending on the fishing method used, environmental conditions, and species (e.g., Parker et al. 1959; Wardle 1978; Wilkie et al. 1996). In certain simulated capture conditions, mortality of sablefish (*Anoplopoma fimbria*)

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was recently shown to reach 100% (Davis et al. 2001). Consequently, as part of the selective fishing policy aimed at conservation through the mandatory live release of nontarget species instituted by the Minister of Fisheries and Oceans Canada in 1998, all British Columbia commercial salmon fishing vessels were required to carry and use fish-recovery boxes ("blue boxes"). The intent was that coho salmon would be revived on board the vessel prior to release, with the expectation that the revived fish would have a better chance of survival, escape predation, and be less likely to be recaptured during commercial fishing, increasing their likelihood of successfully migration and reproduction.

The benefits of using fish-recovery boxes prior to live release in a commercial setting are still uncertain (e.g., Ellis 1964; Thompson et al. 1971; Blewett and Taylor 1999). Perhaps the greatest concern is that, despite efforts at revival, a significant proportion of exhausted salmon can die within 2–8 h, and up to 24 h later, a phenomenon termed postcapture delayed mortality (e.g., Parker and Black 1959; Wardle 1978; Wood et al. 1983). A logistical problem is the slow metabolic recovery from exhaustion in fish compared with amphibians, reptiles, and mammals (Gleeson 1991), a finding that is well established in the fish physiology literature (e.g., Black 1957; Dobson and Hochachka 1987; Milligan 1996). Nevertheless, Milligan et al. (2000) recently showed that a more rapid recovery (2 vs. 6 h) can be promoted in exhausted rainbow trout (*Oncorhynchus mykiss*) if they are allowed to swim moderately fast rather than remain stationary during recovery. Therefore, the possibility exists that commercially caught salmon can recover within approximately 2 h given appropriate holding conditions.

A recent study failed to show appreciable metabolic recovery of coho salmon placed in a blue box (a 50- to 100-L tub with a lid and a running water supply, as required by Fisheries and Oceans Canada) for 30–60 min revival on board commercial salmon fishing vessels (seine, gillnet, and troll) (Farrell et al. 2000). Only plasma K^+ levels recovered significantly. Nonetheless, an encouraging finding was a delayed-mortality rate of only 2.4% (Farrell et al. 2000). The study concluded by criticizing the design of the blue box. Therefore, to specifically address our concerns regarding the recovery-box design, we performed experiments with a Fraser box that incorporated a number of important improvements over the older blue box. Foremost, fish were orientated into flowing water to assist gill ventilation, and the dimensions of the box were such that they limited fish movement, preventing fish from turning around. Also, the rate of water flow was more than ample to meet the estimated maximum oxygen consumption of these adult salmon. Furthermore, an exit door, located at the head end of the recovery box, was in the form of a sluice gate that, once lifted, allowed fish to be returned to the ocean via a water slide, with minimal handling and air exposure. For sampling purposes in the present study, the sluice gate released fish into a trough, where they were rapidly killed. This rapid-sampling procedure greatly reduced concerns expressed in our earlier study about fish handling prior to tissue sampling. In contrast to our earlier study, we obtained conclusive evidence that the physiological status of coho salmon was improved as a result of revival in a Fraser box. Even fish initially ranked as dead when removed from the gillnet were successfully revived. We also performed in-water swim tests on revived fish and we monitored fish for up to 24 h in a netpen to assess postcapture delayed mortality.

Material and methods

Commercial fishing methods

This study was conducted in Alberni Inlet, British Columbia (area 23, subareas 1 and 2), in September and October 1999 on board the CFV *Myshkin*, a commercial gillnet vessel, in collaboration with Fisheries and Oceans Canada. The gillnet used in the study was a paneled 200-fathom, 12.4-cm (4 7/8 in.), 90-mesh Alaska Twist hung at 2.0:1, and 60-fathom 10.2-cm (4 in.), four-strand, 60-mesh Alaska Twist hung at 2.2:1. Both nets had weed lines with 10.2-cm (4 in.) beckets. Up to 260 fathoms of net was used with varying soak times (the soak time is the total time the gillnet was in the water, i.e., from first cork in to last cork out). Soak time was usually ≤40 min and never >70 min. Soak times ≤40 min were used in this study to ensure sufficient numbers of fish in a vigorous condition at capture.

A healthy stock of Alberni Inlet coho salmon was targeted for the experiments. Fish were grouped according to their visually ranked condition at capture. Each fish was given a ranking based on established Fisheries and Oceans Canada categories (category 1 = lively and vigorous with no bleeding; category 2 = lively, vigorous, and bleeding; category 3 = lethargic with no bleeding; category 4 = lethargic and bleeding; category 5 = dead, either flaccid or stiff with no sign of ventilatory movements). These experiments focused only on fish in categories 1, 3, and 5 (hereinafter termed vigorous, lethargic, and asphyxiated, respectively). As it turned out, only three fish were observed to be bleeding as a result of capture and were not used here. The visual ranking category of nonbleeding was confirmed by the hematocrit measurement, which averaged ~50% for all fish sampled (see Table 1), including fish held for 1–24 h post capture. For the experiments that tested the Fraser recovery box, a total of 315 coho salmon (fork length 54–78 cm) were used. Of the total, 176 fish were used for tissue sampling (7–21 fish per treatment group), 102 fish were tested in a swim tunnel (7–15 fish per treatment group), and 2 category 5 fish died during recovery. Another 21 fish recovered in the netpen as part of the assessment of delayed mortality, but were not sampled or swum; they were released alive directly into the ocean. A further 14 fish (category 5) were put in an old-design blue box (see Farrell et al. 2000) prior to transfer to the netpen to assess delayed mortality.

Recovery-box design

The Fraser recovery box was a 40 × 40 × 90 cm darkened wooden box with a centre divider along its length so that a fish could be placed in either side of the box (details of the design can be obtained via www.mypage.uniserve.ca/~fraserjake). A fastening lid, covered on the underside with foam insulation, prevented fish from escaping. Each side of the box had its own water inflow and outflow at either end of the channel (2.54 cm plumbing; flow rate ≥0.6 $L \cdot s^{-1}$). The box was filled with seawater. Preliminary experiments using mixed salmon species during a commercial sockeye salmon opening (June–July 1999) at area 3 (Nass/Portland Canal) were used to test flow rates. A flow rate of 0.1 $L \cdot s^{-1}$ at 9–11°C did not work well, while 0.2 $L \cdot s^{-1}$ improved the speed with which fish became vigorous. Even so, in Alberni Inlet, a flow rate of 0.2 $L \cdot s^{-1}$ did not appear to be effective at 12–16°C and therefore 0.6 $L \cdot s^{-1}$ was used for all experiments. This flow rate was theoretically about twice that needed to meet the estimated maximum oxygen consumption of salmon of this size at this water temperature. Water (12–16°C) was drawn from the ocean at a depth of about 1.5 m by a portable pump. The inflowing water was jetted towards the fish's mouth to provide forced ventilation. The front of the box had

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a vertical sliding sluice gate that, when lifted, acted as a swim-through exit door for the fish. A rubber chute was attached to the sluice gate that acted as a water slide so that the fish could swim in a stream of water down the chute and overboard into a netpen or the ocean. The sluice gate and chute arrangement allowed for rapid transfer of fish with minimal scaling and slime loss, as well as limited air exposure. For tissue sampling, the chute led to a V-shaped trough that had a plastic cone at one end to hold the fish's head. Fish were stunned with a blow to the head within 2 s of release.

A transporter box was used to move fish from the vessel to the swim tunnel. Transporter boxes were half the size of the recovery box (to reduce weight) and held only one fish. In addition, a long rubber sleeve was attached to the sluice gate and used to guide the fish directly into the swim tunnel from the transporter box. Again, the sleeve minimized handling and air exposure.

In-water swimming flume

Swimming performance was measured in the ocean using an open-circuit swimming flume. The flume was fashioned out of 29.8 cm i.d. PVC piping and based on a Brett-type swim tunnel design that was used previously for our studies with adult sockeye salmon and rainbow trout in either the laboratory (Jain et al. 1998; Farrell et al. 1998) or the field (K. Tierney and A.P. Farrell, unpublished data). The section of tubing in which the fish swam was ~2 m long and had three viewing ports of clear polycarbonate, one of which acted as the entry–exit door. Metal grids were placed at either end of this swimming section. A hydraulic motor and a 10-in. propeller generated water flow. Large changes in water velocity were achieved by changing the speed (rpm) of the hydraulic pump. Two hydraulic flow control valves were used to make fine changes in water velocity. A velocity meter (Valeport Marine Scientific Ltd., Dartmouth, U.K.) was placed downstream of the fish to monitor water velocity throughout the experiment. The swim tunnel was submersed in the ocean, adjusted in height, and bolted to the side of a 6-m herring skiff. The operator and the equipment were stationed inside the herring skiff, which was anchored to a log boom to limit wave action.

Netpen design

A 12.2 × 12.1 m netpen was secured to a float near to the fishing site at China Creek, Alberni Inlet. This netpen acted as a protective screen against aquatic mammals for six smaller (4 × 5 × 6 ft; 1 ft = 1.305 m) netpens located inside the larger pen. Fish were held in the smaller netpens for a 24-h recovery period after revival in a Fraser box. Three netpens were used to separate vigorous, lethargic, and "dead" fish from the morning catch, while the other three netpens were similarly used for the afternoon catch. The smaller netpens could be drawn up individually, allowing for easier sampling of fish than the larger one. Some of the fish not used for the tissue sampling and swim tests after recovery in the netpen were released to Alberni Inlet.

Experimental protocols

Tissue sampling

As the net was hauled, fish were quickly and carefully removed. If necessary, a mesh was cut to minimize skin damage. The use of appropriate fish-handling techniques minimized physical damage (e.g., very little scale loss occurred) and air exposure (a matter of seconds). Fish were assigned to 1 of 20 treatment groups based on their visual ranking, length of recovery period (no recovery, either 1 or 2 h revival in a Fraser box, or a 24-h recovery period in a netpen), and type of measurement performed. To simulate the effect of air-exposure during handling of fish on a commercial vessel, an additional group of lethargic fish was deliberately air-exposed for 2 min prior to sampling or being placed in a Fraser box.

Fish allowed no recovery were sacrificed immediately. All other fish were immediately placed in a recovery box on board the vessel (or in a transporter recovery box prior to a swim tests) and were not rehandled until tissues were sampled After a fixed recovery period of either 1 or 2 h, the sluice gate to the Fraser box was opened and the fish was stunned immediately. A skeletal muscle sample (approximately 0.5 × 1.0 × 1.0 cm) was quickly (<35 s) excised from below and slightly to the anterior of the dorsal fin. The muscle sample was instantly frozen between metal tongs that had been precooled in dry ice. The frozen tissue was placed in tin foil and stored on dry ice. Directly following the muscle biopsy, blood was drawn by caudal puncture into a 3-mL Vacutainer (containing lithium heparin) and two heparinized hematocrit tubes were filled immediately from the blood sample. The blood samples were stored on crushed ice for <20 min before being centrifuged on board the vessel for 15 min at 1300 × *g* (Clay Adams Compact II). Hematocrit tubes were centrifuged for 5 min at 8000 rpm in a Clay Adams Readacrit (Parsippany, N.J.). Plasma was aliquoted into 1 mL Eppendorf tubes that were then frozen on dry ice. The muscle and plasma samples were subsequently stored at –80°C until they were analyzed in the laboratory.

For swimming tests, fish were moved in transporter boxes to an in-water swim tunnel using either a small skiff or the vessel. The time taken to transfer fish to the in-water swim tunnel was standardized at 10 min. At the swim tunnel, fish were guided into the swim tunnel inside the rubber sleeve and were given a 10-min habituation period during which the water velocity was 45 cm·s^{-1} for 5 min and 55 cm·s^{-1} for a further 5 min. These velocities (<20% of U_{max} (see below)) were sufficient to orientate the fish into the water current and force slow swimming. Fish were considered to be recovering, so revival time before the swim test was considered to be 20 min, 1 h 20 min, or 2 h 20 min. In addition to fixed recovery periods, vigorous and lethargic fish were allowed to recover for various lengths of time until they were visually assessed as "lively," at which time they were transferred to the in-water swim tunnel for testing. The swim-test protocol involved incremental increases in water velocity of 10 cm·s^{-1} every 2 min until the fish would not swim any faster. If a fish rested on the rear grid, it was encouraged to swim by prodding the tail with a rod inserted through a small hole in the top of the tunnel. Fish were considered fatigued if they rested for >20 s. The maximum swimming velocity for this ramping protocol, U_{max}, was calculated in a manner similar to that used for calculating critical swimming speed (Brett and Glass 1973), i.e., $U_{max} = U_{f-1} + U_f \cdot t$, where U_f and U_{f-1} are the final and penultimate velocity steps and t is the proportion of the 2-min period spent at U_f. U_{max} was adjusted for any solid blocking effect (Bell and Terhune 1970), based on measurements of the fish's dimensions. Fish that refused to swim were recorded as nonswimmers. At the end of the swim test, fatigued fish were gently lifted out of the tunnel and their body dimensions measured prior to release into the surrounding waters of Alberni Inlet.

Netpen recovery and postcapture delayed mortality

Postcapture delayed mortality and physiological status of coho salmon tissues were assessed after a 24-h recovery period. Our earlier study (Farrell et al. 2000) showed a low mortality rate for adult coho salmon placed in a netpen for 24 h, which is expected to occur mostly within 8 h of capture (Wertheimer 1988). Nonetheless, delayed mortality in non-salmonid species is known to occur much later (weeks) after induction of stress (e.g., Olla et al. 1997), and the possibility that delayed mortality could have continued after the 24-h observation period cannot be excluded (see Discussion). Coho salmon were transferred from the Fraser box to the netpen once they had revived sufficiently to maintain an upright position. For tissue sampling, fish were removed from the netpen by quietly drawing it up and individually netting and stunning fish. Fish

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would struggle to a variable extent during this process, but this was unavoidable. To transfer fish to the in-water swim tunnel, it was towed to the netpen. Fish were then individually netted and either placed directly in the swim tunnel or put into a transporter box to assist with the transfer. Fish, especially those ranked as vigorous, struggled to a variable degree during this transfer. Fish were given only a 10-min habituation period before the swim test started.

A total of 87 fish were used in this manner to assess 24-h delayed mortality (i.e., the percentage of surviving fish in a netpen 24-h after capture): 23 fish (14 vigorous and 9 asphyxiated) were used for the swim tests, 41 fish (14 vigorous, 14 lethargic, and 13 asphyxiated) were used for tissue sampling, 21 fish (3 vigorous, 11 lethargic, and 7 asphyxiated) were released alive from the netpen without any tests being performed on them, and 2 fish died during revival.

In addition, a total of 14 asphyxiated fish were used to assess delayed mortality using the old-design blue box. Seven of these fish were not revived in the blue box and one fish escaped from the blue box. Therefore, only six fish were transferred to the netpen.

Analytical techniques

The physiological status of fish was assessed by measuring muscle glycogen, lactate, glucose, adenosine triphosphate (ATP), and phosphocreatine (PCr) levels, plasma lactate, glucose, and cortisol levels (indicators of exhaustion and stress), hematocrit (an indicator of bleeding and stress), and plasma osmolality and ion (Na^+, K^+, and Cl^-) concentrations (indicators of ionic and osmotic imbalance).

Plasma

Plasma lactate and glucose concentrations were measured using a YSI 2300 lactate/glucose analyzer (Yellow Springs Instruments). Plasma samples were thawed immediately before use, vortexed for 30 s, spun in a centrifuge for 2 min at 2000 rpm, and then aspirated into the analyzer. The analyzer was set to automatically calibrate after every five measurements (precision was 0.2 mmol·L^{-1} for lactate and 0.1 mmol·L^{-1} for glucose). Duplicate samples were within 2% of each other. For ion analysis, plasma samples were thawed, vortexed, and centrifuged for 5 min immediately before analysis. Plasma chloride concentrations were measured in duplicate using a model 4425000 Haake Buchler digital chloridometer. The measurements were repeated if disagreement between duplicates was greater than 2.5 mmol·L^{-1}. The chloridometer was checked against a chloride standard (100 mmol·L^{-1} Cl^-) before and during the process (approximately every 10 duplicates). Plasma sodium and potassium concentrations were measured using a model 510 Turner flame photometer. Plasma aliquots (5 µL) were diluted 1:200 with a prepared 15 mmol·L^{-1} lithium diluent for analysis. The machine was calibrated prior to use and checked against a standard approximately every six samples. Measurements were repeated if the disagreement between duplicates was >2%. Osmolality was measured in duplicate on 10-µL samples using a model 5500 Wescor Vapour Pressure meter. The thermocouple heads were cleaned periodically to maintain consistency. Measurements were repeated if the disagreement between duplicates was >3%. Plasma cortisol concentrations were measured in duplicate using 96-well ELISA kits (Neogen Corp., Lexington, Ky.) and suitable dilutions of the plasma.

Muscle

Muscle tissue was powdered under liquid nitrogen using a precooled mortar and pestle. Approximately 500 mg of powdered tissue was added to a precooled, preweighed vial containing 1 mL of ice-cold 0.6 N perchloric acid (PCA). Each vial was reweighed and made up to a final dilution of seven volumes (vol·wt^{-1}). The PCA extracts were homogenized on ice for 2 × 15 s at maximum speed with an Ultraturex tissue homogenizer. An aliquot was immediately frozen in liquid nitrogen for determination of glycogen. The remaining PCA extract was then centrifuged for 2 min at 13 000 rpm in a microcentrifuge. A known volume of supernatant was immediately removed and neutralized with a saturated potassium carbonate solution. The neutralized extracts were stored at –80°C until analysis. Glycogen was digested with amyloglucosidase (Bergmeyer 1983) and glucosyl units were determined on the YSI 2300 StatPlus lactate/glucose analyzer. Final glycogen levels were determined after subtracting muscle glucose values. Muscle glucose and lactate concentrations in the extracts were determined with the analyzer as above. Muscle PCr and ATP concentrations were determined enzymatically by following the production of nicotinamide adenine dinucleotide phosphate at 340 nm (Bergmeyer 1983).

Statistical analysis

Given the well-established physiological changes associated with exhaustive exercise in salmonids (see Milligan 1996), the main interest was to determine whether or not variables recovered over time. Also of interest were possible differences among the vigorous, lethargic, and air-exposed groups of fish. Tests for both such differences were done through a two-factor analysis of variance (JMP, SAS Institute Inc., Cary, N.C.) with fixed effects for recovery time and fish condition, with interactions, and with a 5% significance level. All analyses were followed by appropriate multiple comparison tests to determine which means were significantly different (with Tukey or Bonferroni adjustments to reduce the experimentwise error rate to at most 5%). The swim-test data were also analyzed with an analysis of covariance, with fish condition as a factor and recovery time as a covariate.

Results

Visual observations

Vigorous fish were not refractory; they needed to be held firmly during transfer and remained active inside the Fraser box. The variable recovery period for vigorous fish prior to the swim test averaged 30 min (N = 8). Vigorous fish periodically thrashed about in the recovery box when left for fixed recovery periods. Lethargic fish, in contrast, were exhausted and ventilating on capture and recovered to a vigorous state in the Fraser box. The variable recovery period for lethargic fish prior to the swim test averaged 59 min (N = 8). Most "dead" fish were revived (29 out of 31 fish) and since only 6.5% actually died, we termed these fish asphyxiated. Asphyxiated fish, including those that were quite stiff at capture, resumed ventilation usually within 10 min of being placed in a Fraser box, and became moderately active after about 45 min.

Postcapture delayed mortality was monitoring in 87 fish following initial revival in a Fraser box. No mortality of lethargic or vigorous fish occurred (N = 56; 28 fish were used for tissue sampling, 14 fish were released without testing, and 14 fish were used for swim tests). Only two asphyxiated fish died, one in a Fraser box and one overnight in the netpen. Therefore, the overall 24-h postcapture delayed mortality rate was only 2.3%.

Out of 14 asphyxiated fish placed in a blue box, 7 died and 1 escaped, a revival rate of 50%. Out of the six revived fish transferred to a netpen, five survived for 24 h. Therefore, the 24-h postcapture delayed mortality rate for asphyxiated fish (either 62% (8/13 fish) or 57% (8/14 fish)) was

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almost 10-fold higher for the blue box than for the Fraser box.

Physiological status of coho salmon at capture and during recovery

Plasma and tissue variables

The physiological status of muscle and plasma sampled from all fish combined (Table 1) leaves no doubt that these wild coho salmon were physiologically exhausted and stressed as a result of capture. Muscle lactate (53.7 mmol·L^{-1}) exceeded the level reported for severely exhausted rainbow trout by nearly 70%, muscle glycogen and PCr levels were low, and plasma cortisol levels were elevated.

Overall, fish revival in a Fraser box caused significant ($P < 0.05$) changes in hematocrit, plasma osmolality, plasma glucose, lactate, cortisol, Na^+, and Cl^- concentrations, and muscle lactate, glucose, and PCr concentrations (Table 1). Some of the changes occurring after 1 h were interpreted as signs of physiological recovery. Specifically, and compared with the variables for fish that were sampled immediately after capture, there were significant increases in muscle PCr and plasma glucose concentrations and a decrease in muscle lactate concentration. Significant recovery was also evident after 2 h in the form of a significant decrease in hematocrit, an increase in muscle glucose concentration, and a further decrease in muscle lactate concentration, as well as decreases in osmolality and plasma cortisol, Na^+, and Cl^- concentrations between 1 and 2 h. The decrease in plasma Cl^- concentration could also represent partial ionic compensation for increased plasma lactate concentration (see McDonald and Milligan 1997). Thus, while muscle metabolites recovered during the first hour of revival, plasma ion concentrations and osmolality were slower to recover, since there were significant increases in osmolality and plasma lactate, cortisol, and Na^+ concentrations after 1 h (Table 1). Overall, recovery time had no significant effect on muscle glycogen and ATP concentrations and plasma K^+ concentration (Table 1).

The physiological changes associated with revival of vigorous, lethargic, and air-exposed fish groups are summarized separately in Figs. 1, 2, and 3, respectively. All three groups of fish exhibited a similar pattern of change during revival. Surprisingly, however, statistically significant differences as a function of recovery time within the fish groups were limited to ionic and osmotic variables. Vigorous fish had a significantly decreased muscle lactate concentration after 2 h and plasma Na^+ concentration was no longer significantly elevated (Fig. 1). Plasma cortisol levels increased significantly in all three fish groups after 1 h revival. However, the limited changes over time within each treatment group should not detract from the overall finding that coho salmon showed significant physiological recovery.

Statistically significant differences between vigorous and lethargic fish and between lethargic and air-exposed lethargic fish were limited to osmotic and ionic variables (Figs. 1 and 2). Specifically, plasma osmolality and plasma Na^+ concentration were significantly higher in lethargic than in vigorous fish after 1 h recovery, while Na^+ and Cl^- concentrations were both higher in lethargic fish after 2 h recovery. Thus, lethargic fish appeared to undergo a greater ion-osmoregulatory disturbance than vigorous fish. Though the difference was not sta-

Table 1. Effect of revival time on plasma and muscle variables in mature wild coho salmon (all fish independent of visual ranking) caught by commercial gillnet vessel: a comparison between no revival ("none"), 1- or 2-h revival periods in a Fraser recovery box on board the fishing vessel, and a 24-h revival period completed in a netpen.

					Significance[b]			
Response variable	None[a]	1-h[a]	2-h[a]	24-h[a]	None vs. 1-h revival	None vs. 2-h revival	1-h vs. 2-h revival	2-h vs. 24-h revival
Plasma chloride (mmol·L^{-1})	144.5 (0.7)	145.6 (1.1)	141.2 (1.0)	140.1 (0.72)	ns	**	***	ns
Plasma sodium (mmol·L^{-1})	168.6 (0.9)	179.6 (1.1)	174.1 (1.1)	160.1 (0.4)	***	***	***	***
Plasma potassium (mmol·L^{-1})	3.30 (0.26)	3.13 (0.20)	3.70 (0.26)	1.73 (0.16)	ns	ns	ns	***
Osmolality (mosmol)	355.2 (4.0)	379.5 (3.7)	367.6 (2.0)	330.2 (2.1)	***	*	**	***
Hematocrit (%)	52.7 (0.01)	50.1 (0.01)	49.0 (0.01)	47.5 (0.01)	ns	*	ns	ns
Plasma lactate (mmol·L^{-1})	10.5 (0.8)	24.2 (0.9)	23.0 (0.8)	1.91 (0.19)	***	***	ns	***
Plasma cortisol (ng·mL^{-1})	379.6 (45.6)	1271 (75.4)	1083 (71.6)	406.3 (45.1)	***	**	*	***
Plasma glucose (mmol·kg^{-1})	5.27 (0.20)	7.68 (0.35)	6.90 (0.27)	5.00 (0.72)	***	***	ns	***
Muscle lactate (mmol·kg^{-1})	53.7 (1.7)	39.9 (1.3)	30.1 (1.3)	20.1 (1.2)	***	***	***	***
Muscle glucose (mmol·kg^{-1})	2.37 (0.11)	2.11 (0.12)	2.58 (0.08)	0.89 (0.09)	ns	ns	**	***
Muscle glycogen (mmol·kg^{-1})	4.51 (1.79)	5.75 (0.93)	8.71 (2.27)	12.9 (2.50)	ns	ns	ns	ns
Muscle ATP (mmol·kg^{-1})	4.58 (0.48)	5.20 (0.44)	5.50 (0.44)	6.16 (0.63)	ns	ns	ns	ns
Muscle phosphocreatine (mmol·kg^{-1})	8.24 (0.65)	12.1 (1.3)	13.4 (1.1)	14.9 (1.4)	*	***	ns	ns

[a]Least-squares means with standard error of the mean in parentheses (N = 44–55 fish for plasma variables and N = 28–33 fish for tissue variables).
[b]Two-way analysis of variance with interactions (α = 0.05 with additional protection for multiple comparisons); ns, not significant; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. Note that for Na^+ and Cl^- levels, fish condition was a significant factor (see the text), but there was no interaction with recovery time. Also, for K^+ levels and osmolality the interaction between fish condition and recovery time was significant (see the text).

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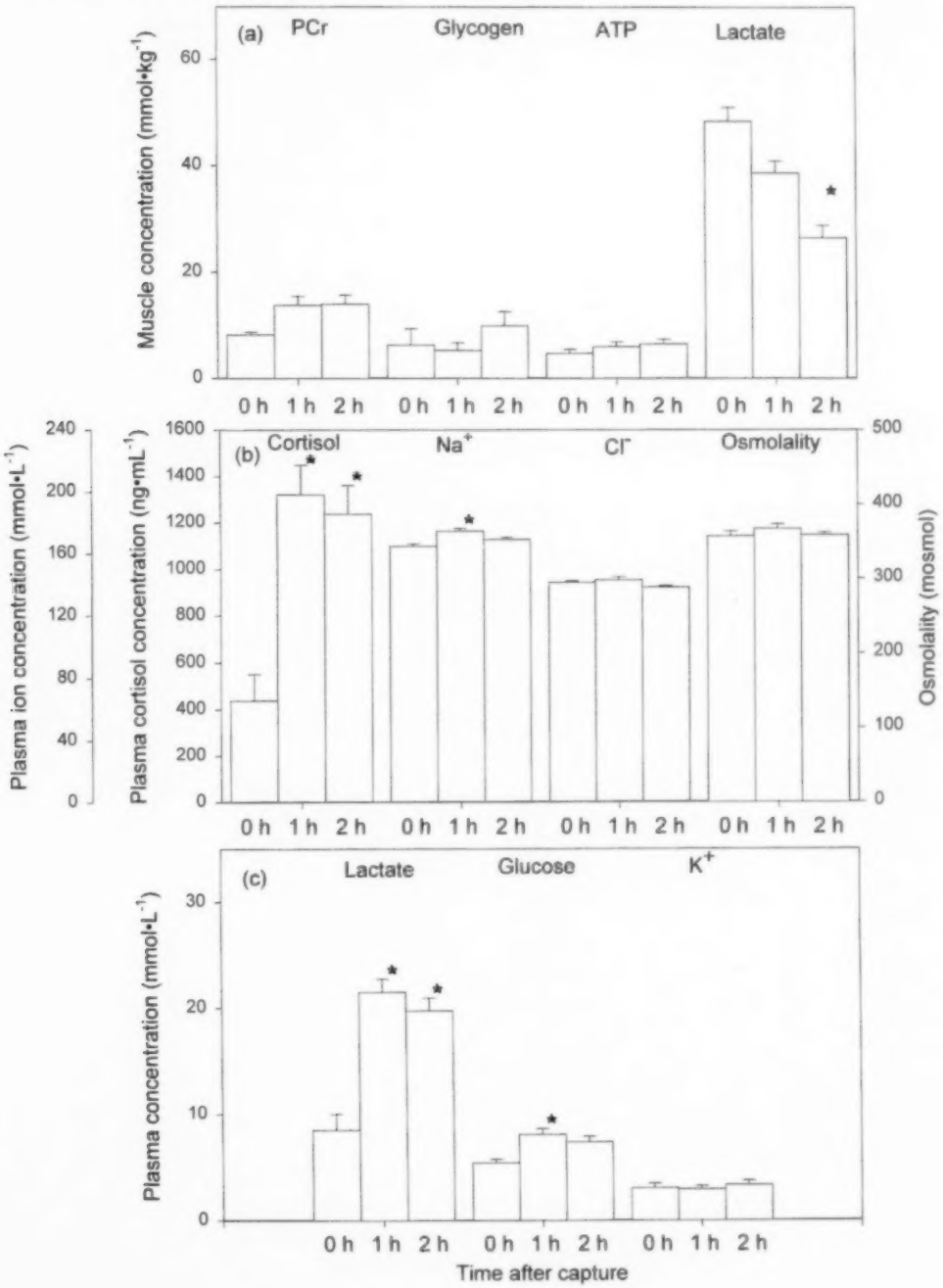
Fig. 1. Effect of recovery time on the physiological status of adult wild coho salmon (*Oncorhynchus kisutch*) captured by a commercial gillnet vessel and visually ranked as vigorous fish at capture (0 h). Muscle and plasma variables were measured after revival in a newly designed Fraser recovery box after either 1 h or 2 h. Values are presented as the mean ± standard error of the mean for 7–20 fish. An asterisk denotes a statistically significant ($P < 0.05$) difference from the respective value at capture. There were no statistically significant differences between the two recovery times.



tistically significant, vigorous fish tended to have initially lower plasma and muscle lactate levels and higher muscle PCr and glycogen levels, which recovered faster than those of lethargic fish. Two minutes of deliberate air exposure of lethargic fish had little effect on the variables measured. In air-exposed fish compared with lethargic fish, only the plasma

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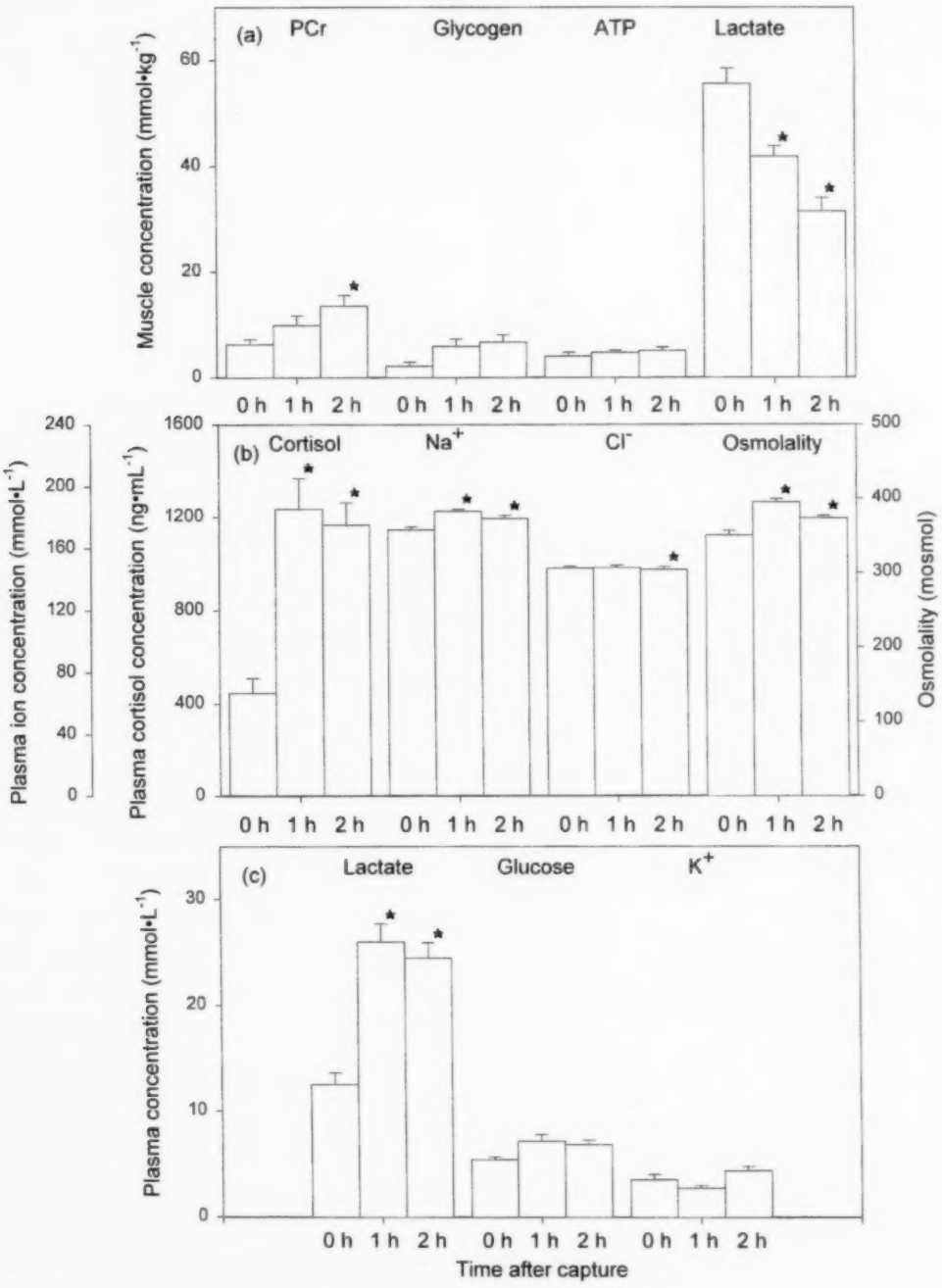
Fig. 2. Effect of recovery time on the physiological status of adult wild coho salmon captured by a commercial gillnet vessel and visually ranked as lethargic fish at capture (0 h). Muscle and plasma variables were measured after revival in a newly designed Fraser recovery box after either 1 h or 2 h. Values are presented as the mean ± standard error of the mean for 7–20 fish. An asterisk denotes a statistically significant ($P < 0.05$) difference from the respective value at capture. There were no statistically significant differences between the two recovery times.



Cl^- level was significantly lower after 2 h. The initial muscle PCr concentration tended to be higher and muscle glycogen levels tended to be lower with air exposure.

The physiological status of coho salmon after 24 h (Table 1, Fig. 4) clearly shows that recovery continued in the netpen. Overall plasma lactate, glucose, Na^+, and K^+ levels, osmolality, and muscle lactate and glucose levels were all significantly lower after 24 h than after 2 h recovery (Ta-

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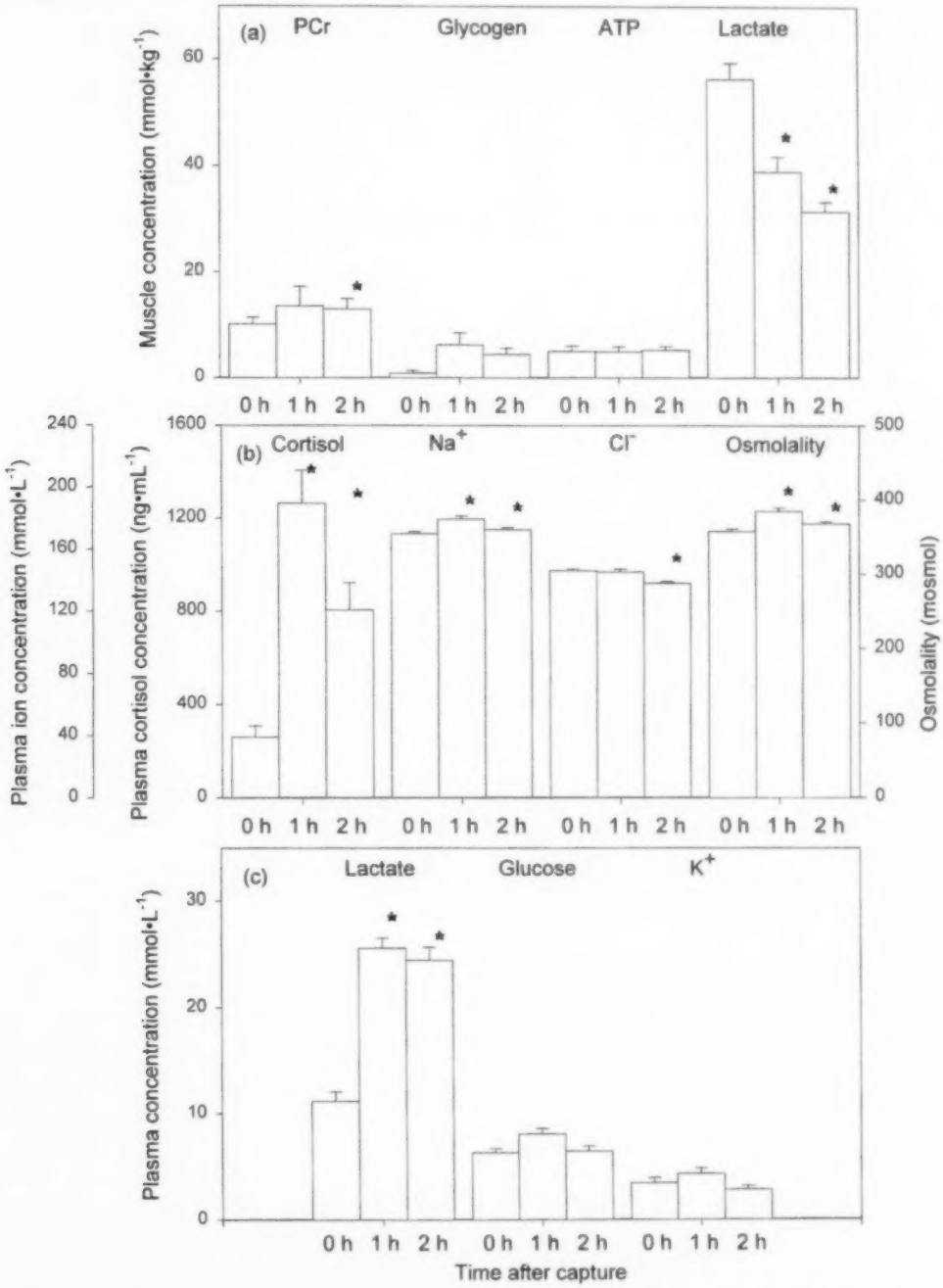
Fig. 3. Effect of recovery time on the physiological status of adult wild coho salmon captured by a commercial gillnet vessel and visually ranked as lethargic fish at capture (0 h) and then deliberately air-exposed for 2 min. Muscle and plasma variables were measured after revival in a newly designed Fraser recovery box after either 1 h or 2 h. Values are presented as the mean ± standard error of the mean for 7–20 fish. An asterisk denotes a statistically significant ($P < 0.05$) difference from the respective value at capture. There were no statistically significant differences between the two recovery times.



ble 1). Plasma cortisol decreased significantly to a level similar to that at capture, but hematocrit, plasma Cl^- level, and muscle glycogen, ATP, and PCr levels did not change significantly (Table 1). That the muscle lactate level apparently remained elevated at around 20 mmol·kg^{-1} is a concern, but this could have resulted directly from the fish-capture method, which caused the netpen fish to struggle before sampling. Physiological recovery was also significant for

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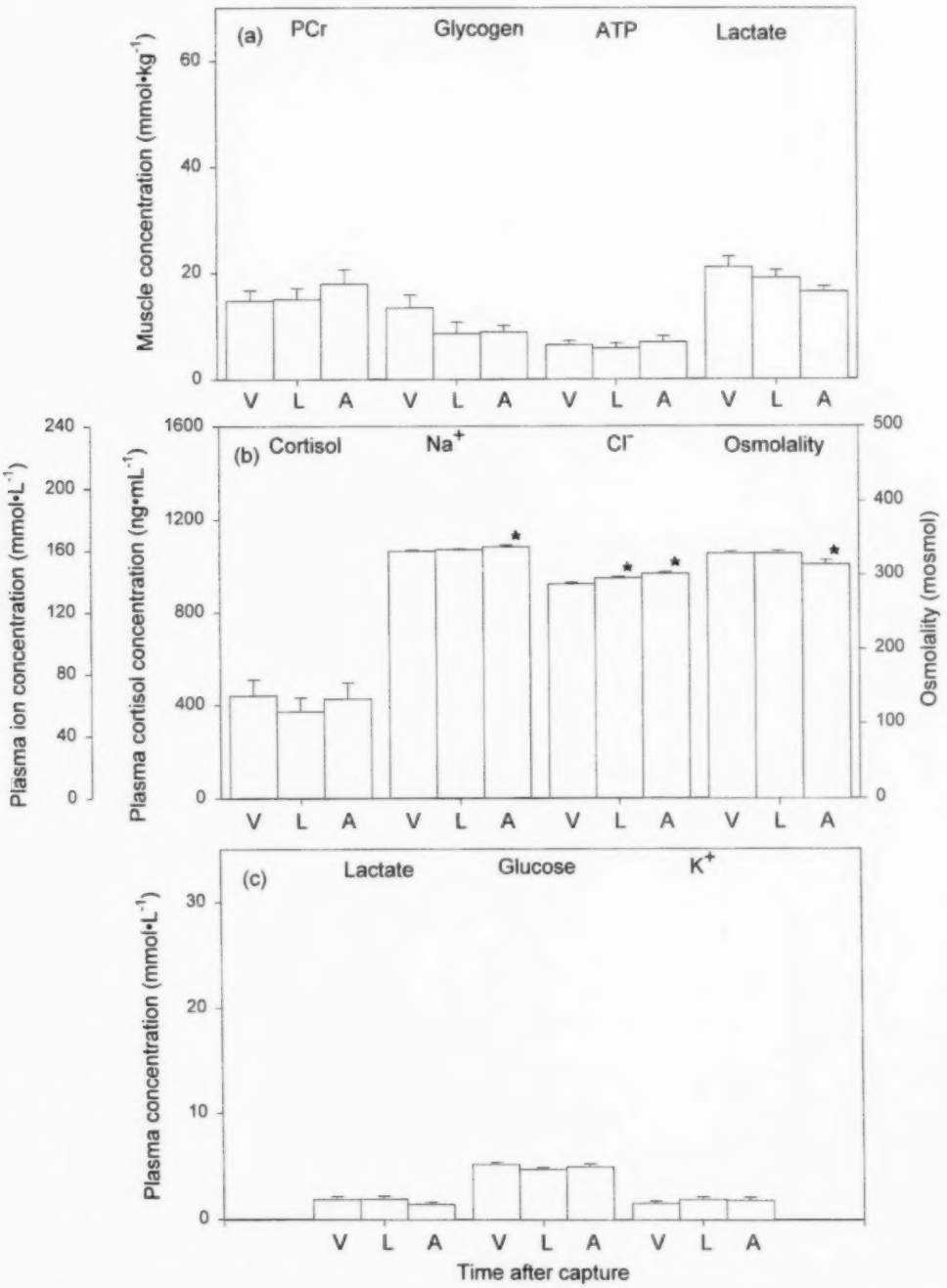
Fig. 4. Physiological status of adult wild coho salmon that recovered in a netpen for 24 h after capture by a commercial gillnet vessel. Fish were visually ranked at capture and before revival as either vigorous (V), lethargic (L), or asphyxiated (A). Muscle and plasma variables were measured after initial revival in a newly designed Fraser recovery box followed by transfer to the netpen. Values are presented as the mean ± standard error of the mean for 7–20 fish. An asterisk denotes a statistically significant ($P < 0.05$) difference from the corresponding value for a vigorous fish. A cross denotes a statistically significant ($P < 0.05$) difference between lethargic and asphyxiated fish.



vigorous fish (Fig. 4); plasma lactate, glucose, Na^+, and K^+ levels, osmolality, and muscle glucose level were all significantly ($P < 0.05$) lower after 24 h than after 2 h recovery. Similarly, for lethargic fish, muscle lactate and glucose levels, plasma lactate, glucose, Na^+, and K^+ levels, and osmolality were all significantly ($P < 0.05$) lower after 24 h

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Table 2. Ramp-velocity swim-test performance for mature wild coho after revival on board a commercial gillnet fishing vessel.

Initial fish condition	Revival period[a]	Percentage of fish that swam to U_{max}	U_{max} ($cm \cdot s^{-1}$)	U_{max} ($BL \cdot s^{-1}$)	Percentage of predicted U_{max} capacity	Swim duration (min)
Vigorous	20 min (13)	69	179 ± 9.0	2.76 ± 0.13	93	31.3 ± 1.7
	50 min (8)	75	173.2 ± 5.3	2.80 ± 0.11	94	30.8 ± 1.0
	1 h 20 min (10)	100	187 ± 8.4	2.97 ± 0.16	100	32.7 ± 1.8
	24 h (14)	79	125 ± 6.4	1.98 ± 0.08	67	22.7 ± 2.3
Lethargic	20 min (15)	87	150 ± 9.3	2.22 ± 0.12	75	27.0 ± 1.3
	59 min (7)	71	152 ± 19.6	2.06 ± 0.18	69	24.1 ± 2.2
	1 h 20 min (14)	93	168 ± 10.7	2.56 ± 0.16	86	31.1 ± 1.7
	2 h 20 min (12)	92	161 ± 8.6	2.46 ± 0.15	83	29.0 ± 2.0
Apparently dead	24 h (9)	78	143 ± 13.8	2.32 ± 0.24	78	28.5 ± 3.1

[a]Numbers in parentheses indicate the number of fish put into the swim flume for testing.

than after 2 h recovery. Significant differences among vigorous, lethargic, and asphyxiated fish were limited to plasma ion concentrations and osmolality (Fig. 4). Specifically, the plasma Cl^- level was significantly lower in vigorous than in lethargic fish, while plasma Na^+ and Cl^- levels were significantly lower and osmolality was significantly higher in vigorous than in asphyxiated fish. Osmolality was also significantly higher in lethargic fish than in asphyxiated fish.

Swimming performance

The majority of coho salmon, including those tested immediately after capture, were able to perform a ramp-velocity swim test in the ocean (Table 2). Out of 78 fish, 61 completed a swim test, a 78% success rate. The combined success rate for vigorous fish (81%; $N = 31$) did not differ from that for lethargic fish (77%; $N = 47$). However, after a 1 h 20 min recovery period, all vigorous fish and all but one of the lethargic fish successfully completed a swim test.

Coho salmon swam for at least 27 min and reached speeds >1.98 $m \cdot s^{-1}$ (>2.2 body lengths (BL)$\cdot s^{-1}$) after revival in a Fraser box for up to 2 h 20 min (Table 2). In particular, vigorous fish swam for over 30 min and reached speeds of up to 2.97 $BL \cdot s^{-1}$ after being revived for 1 h 20 min. U_{max} did not change significantly with recovery time ($P = 0.295$) for either vigorous or lethargic fish. Compared with vigorous fish, lethargic fish tended to swim for shorter times and have a lower U_{max} ($P = 0.007$) for a recovery time of <1 h.

Vigorous and asphyxiated coho salmon were also tested after a 24-h recovery period. Their U_{max} values and total swim times were not significantly different. However, the swimming performance of the vigorous fish (1.98 $BL \cdot s^{-1}$) was significantly lower than that of vigorous fish tested after a 2 h 20 min recovery period (2.97 $BL \cdot s^{-1}$), a difference probably attributable to the difficulty of handling vigorous fish from the netpen (see the Discussion).

Discussion

Can commercially caught coho salmon be revived?

This is our second study broadly examining the physiological status of wild adult coho salmon immediately after capture by commercial salmon vessels. The primary focus of both the present and previous (Farrell et al. 2000) studies was to ascertain whether or not fish recovered physiologically when placed in a revival box. The present study with a Fraser box was particularly important because the blue-box design was shown previously to be ineffective at promoting significant metabolic recovery. In contrast to the results of our previous work with the blue box, our major conclusion is that a combination of soak times ≤70 min in duration, careful fish handling, and fish revival for up to 2 h in a Fraser box on board a commercial gillnet vessel promoted significant metabolic, ionic, and osmotic recovery. Furthermore, metabolic recovery was sufficiently quick that the majority of revived coho salmon could complete a ramp-velocity swim test within 20 min of capture and reach velocities >1.5 $m \cdot s^{-1}$. Thus, despite being initially exhausted and stressed as a result of capture, revived coho salmon were able to swim well. Perhaps the most pronounced benefit of the Fraser box was the successful revival of asphyxiated fish (those initially ranked as dead at capture), probably because it assisted gill ventilation when asphyxiated fish had stopped breathing for themselves. As a result, postcapture delayed mortality was only 2.3% (2 out of 87 fish) after 24 h of observation. Moreover, the Fraser box was almost 10 times more effective in reviving asphyxiated fish (only 6.5% mortality in this category of fish) than the older design blue box (at least 57% mortality after 24 h of observation). Therefore, we can conclude that the new design features of the Fraser box promoted revival of exhausted coho salmon more than the older design of blue box. The following discussion expands on these important findings.

Physiological status of fish at capture in the context of commercial salmon gillnet fishing

In the context of commercial gillnet fishing, our data suggest that live release of commercially caught nontarget coho is possible, provided appropriate fishing, handling, and recovery methods are employed. We found revival and improved physiological status in the vast majority of coho salmon. Therefore, had they been returned to the ocean, there was a high expectation that the revived fish could have completed their spawning migration, especially given the positive findings regarding swimming performance. Despite this optimism, the relevance of our findings to commercial salmon fishing has to be scrutinized. Had we used a normal commercial sockeye salmon fishing operation where coho salmon were by-catch, we were concerned that we might have jeopardized the statistical power of the experiments because of low sample sizes (fishing opportunities can be short and unpredictable and the incidence of coho salmon by-

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catch is normally low). Instead, to ensure sufficient coho salmon for each of the numerous treatment groups, we chose to target a healthy stock of coho salmon. We also employed modified commercial fishing gear and methods. Consequently, the present techniques and results still need to be validated in a commercial fishing operation with coho salmon as by-catch and with more than one commercial fishing vessel.

A potentially serious concern with targeting fish for experimental purposes is the possibility that inadvertently, captured fish were not as severely stressed as commercial by-catch might be and this in itself permitted successful fish revival. However, this clearly was not the case. Using both visual and physiological measures, the coho salmon captured for this study were severely stressed and exhausted when they were hauled on board the vessel. Some fish were lethargic, while others were asphyxiated and appeared dead. Furthermore, the physiological data are clearly consistent with the expected profile for a severely exhausted fish (Milligan 1996). In particular, muscle lactate levels were as extreme as any measured previously either in rainbow trout chased to severe exhaustion or in Atlantic salmon (*Salmo salar*) angled to exhaustion (Booth et al. 1995; Wilkie et al. 1996; Brobbel et al. 1996). Also, muscle glycogen levels were below detection limits in a number of fish at capture, especially the air-exposed fish. In addition, many variables were similar to those in our earlier study with a blue box. For example, at capture, plasma Na^+ levels (171.4 versus 168.6 $mmol \cdot L^{-1}$), osmolality (350.5 versus 355.2 mosmol), and muscle lactate levels (54.7 versus 53.7 $mmol \cdot kg^{-1}$) were comparable in the earlier study (see Table 1 in Farrell et al. 2000) and the present study, respectively. However, muscle PCr (2.36 versus 8.24 $mmol \cdot kg^{-1}$) and glycogen (2.04 versus 4.51 $mmol \cdot kg^{-1}$) levels were higher in the present study. There are two possible reasons for these differences. Foremost, the tissue-sampling protocol in the present study was more rapid and less stressful, and higher muscle PCr and glycogen levels could reflect fewer sampling artifacts in the present study. Second, by reducing the physical trauma to the fish, the modified fishing and handling methods may have been a contributing factor. However, rather than this being a limitation to the main conclusion of the study, we suggest that gillnet soak times of ≤70 min, use of an appropriate type of gillnet, and careful fish handling on board should be considered along with the Fraser box as components of the fishing methods, to ensure effective coho salmon revival. Furthermore, we recommend that the low mortality rates obtained in our controlled study (6.5% for asphyxiated fish and 2.3% overall) should be used as benchmarks when revival methods are tested and refined in a real-life commercial sockeye salmon gillnet fishery where coho salmon are by-catch. While "short" soak times were clearly integral to successful fish revival, our experiments do not directly address the question of how short they should be. Future experiments should be aimed at resolving this important question.

The visual ranking of fish as "dead" was clearly inappropriate when coho salmon were handled in the manner we used here. Of the 31 fish ranked as dead, 30 were revived in a Fraser recovery box and only 1 of these showed delayed mortality in the netpen. However, this high success rate in reviving asphyxiated fish was not observed with the older design blue box. We return to this point later in the Discussion.

What was the extent of physiological recovery during fish revival?

Fish revival resulted in a clear and significant return to a more normal status for muscle metabolites, based on what is known from laboratory experiments with rainbow trout. As expected, muscle lactate levels decreased during revival, while muscle glycogen, ATP, and PCr reached stable levels. While extensive comparisons of these physiological variables have been made elsewhere (Milligan 1996; Kieffer 2000; Farrell et al. 2000), it is very important to note that a number of the variables we measured after 1 h recovery were different to those measured in our earlier study using a blue box (Farrell et al. 2000). In particular, metabolic, ionic, and osmotic disturbances generally were less for coho salmon placed in a Fraser box than for those placed in a blue box (e.g., plasma Na^+ (179.6 versus 190.9 $mmol \cdot L^{-1}$) and plasma Cl^- levels (145.6 versus 151.9 $mmol \cdot L^{-1}$), osmolality (355.2 versus 390.7 mosmol), and muscle lactate levels (39.9 versus 53.9 $mmol \cdot kg^{-1}$)), while levels of muscle metabolites were higher (e.g., muscle glycogen (5.75 versus 2.02 $mmol \cdot kg^{-1}$) and muscle PCr (12.1 versus 1.14 $mmol \cdot kg^{-1}$)) (this study and Table 1 in Farrell et al. 2000). However, some of the variables (hematocrit, plasma lactate, K^+, and glucose levels, and muscle glucose level) were comparable between the two studies.

The elevation in plasma cortisol levels during coho salmon revival in a Fraser box is new information and clearly shows that the fish remained severely stressed despite their metabolic recovery. We are unsure whether the increase in plasma cortisol during fish revival represents solely the expected increase in plasma cortisol levels that occurs 20–30 min following a stress or is an indication that the recovery box was an additional stressor. Some fish certainly thrashed around in the Fraser box because they were sufficiently well recovered to try to escape prior to the set sampling time, and this activity certainly could have further increased cortisol levels. Nevertheless, plasma cortisol levels decreased significantly in the second hour of recovery and had returned to the levels measured at capture following the 24-h recovery. Interestingly, coho salmon captured by commercial troll-fishing methods, placed in a cage alongside the vessel, and sampled approximately 2 h later had plasma cortisol levels that were not nearly as elevated as observed here (A.P. Farrell, P.E. Gallaugher, and R. Routledge, Simon Fraser University, unpublished data), even though the values at capture were in the same range. Similarly, Milligan et al. (2000) showed that swimming during recovery lowers plasma cortisol levels and promotes metabolic recovery of exhausted rainbow trout. Therefore, we suspect that confining coho salmon in a Fraser box does create an additional stress that elevates plasma cortisol levels. However, this stress must be weighed against the benefits of partial metabolic recovery and the revival of asphyxiated fish, benefits that were not apparent in the earlier study with a blue box. In any use of the Fraser box, therefore, variable recovery times linked to the activity observed in the fish should be considered, so that metabolic recovery can be maximized

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and stress minimized and fish can be returned to a situation when and where they can swim at a moderate speed. Perhaps ventilation rate could be used as an index of the decline in metabolic rate during recovery (e.g., Farrell et al. 1998).

An important question is whether the coho salmon were ever fully recovered. We lack reliable physiological data on rested adult coho salmon that would allow us to reach a definitive answer to this question, so for comparisons we must draw on data from adult salmonids of other species. A second problem is the large individual variation in two of the key muscle metabolites (PCr and glycogen). This variability certainly decreased statistical power and hampered the statistical resolution among mean values, which in some cases varied severalfold during revival. Interestingly, while netpen recovery decreased the individual variability in muscle lactate levels, osmolality, and plasma lactate, glucose, Na^+, and K^+ levels, it did not do so for PCr and glycogen levels (variability in hematocrit and muscle ATP and muscle glucose levels was already quite low). For example, PCr levels ranged from 2 to 20 mmol·kg^{-1} at capture, from 3 to 27 mmol·kg^{-1} in the Fraser box, and from 4 to 31 mmol·kg^{-1} in the netpen. This suggests to us that the low PCr level in some individuals came about secondarily from fish re-exhausting themselves either in the recovery box prior to an assigned sample time or when captured from the netpen.

Routine muscle PCr levels are 25–35 mmol·kg^{-1} in adult Atlantic salmon (Booth et al. 1995; Wilkie et al. 1996; Burgetz et al. 1998) and rainbow trout (Scarabello et al. 1991; Milligan 1996), and they are usually restored within 2–4 h following exhaustion. Therefore, PCr levels in revived coho salmon (12–15 mmol·kg^{-1}) suggest at least 50% recovery of this important fuel. Some individuals with PCr levels >20 mmol·kg^{-1} after a 2-h revival period may have approached full recovery of PCr. Curiously, for netpen recovery, asphyxiated fish had the highest average PCr level (21.2 mmol·kg^{-1}) and yet were clearly the most debilitated at capture. Since these fish were rather inactive when removed from the netpen, we suspect that PCr recovery was underestimated to some degree in vigorous fish sampled from the netpen as a result of fish struggling.

The muscle glycogen level (8.7 mmol·kg^{-1}) was not fully restored in the recovery box because higher levels were measured following netpen recovery. It is well established that glycogen recovery is slower than PCr recovery (Milligan 1996; Pagnotta and Milligan 1991). Also, glycogen recovery is reportedly slower at low temperature (Wilkie et al. 1997) and when muscle lactate levels exceed 56 mmol·kg^{-1} (Stevens and Black 1966), as was often the case here. Depending on the feeding status of the fish, muscle glycogen levels in salmonids typically vary between 10 and 40 mmol·kg^{-1} (e.g., Hochachka and Sinclair 1962; Scarabello et al. 1991; Kieffer and Tufts 1998). Given that muscle lactate levels increased to over 50 mmol·kg^{-1}, we would expect muscle glycogen to be normally around half of this value (i.e., 25 mmol·kg^{-1}) in these coho salmon. Consequently, our finding that the muscle glycogen level was restored to 17.1 mmol·kg^{-1} in vigorous fish and 24.0 mmol·kg^{-1} in asphyxiated fish suggests that muscle glycogen levels were probably close to being fully restored 24 h post capture.

The corollary of muscle glycogen not being fully restored in the recovery box is that muscle lactate levels were significantly elevated. We anticipated that muscle lactate could recover to levels as low as 10 mmol·kg^{-1} (Milligan et al. 2000) but, as noted above, this was not the case. Nevertheless, even with some minor uncertainties, we measured significant metabolic recovery under these difficult field conditions. Metabolic recovery generally preceded ionic and osmotic recovery during the first 2 h. Nevertheless, after a 24-h recovery, in coho salmon held in netpens, plasma lactate and K^+ levels were apparently restored to 1.7 mmol·L^{-1} and plasma cortisol was restored to a level comparable to that measured immediately after capture. (The low plasma K^+ level at 24 h is comparable to routine plasma levels in rested fish, which suggests to us that the elevated plasma K^+ levels post capture were caused by exhaustive exercise and not by contamination from muscle tissue, something that is possible when blood is sampled from caudal vessels.) The plasma cortisol levels we measured here for adult coho salmon in seawater were an order of magnitude higher than those in rested juvenile salmonids in fresh water (10–60 ng·mL^{-1}). However, migrating adult Pacific salmon have been characterized as having a proliferation of interrenal tissue and plasma corticosteroid levels 3–9 times higher than in immature salmon (e.g., Robertson et al. 1961). Thus, plasma cortisol levels in mature coho salmon may be routinely higher than those we have come to expect in freshwater salmonids (see Milligan 1996), but this issue will not be resolved until studies with arterial cannulae are performed on rested adult coho salmon.

Kieffer and Tufts (1998) showed that fish size had an influence on metabolic recovery after exhaustion. We did not systematically investigate this possibility for two reasons. First, the size difference in our fish was only 44% compared with a 10-fold difference in the earlier study. Second, the initial state of exhaustion was not controlled in the same manner as in Kieffer and Tufts (1998). Thus, in the present study, the possibility that fish size could play a factor in metabolic recovery is not discounted. Rather, it is unlikely that the present experimental design would resolve such effects.

Most revived fish apparently swam surprisingly well after only a short revival period. Even so, it is important to examine how well the fish swam. U_{max} was measured in a novel, field-based swim test because this did not take as long to conduct as a conventional critical swim speed (U_{crit}) test. Unfortunately, there are no published values for either U_{max} or U_{crit} for adult coho salmon against which the present findings can be compared. However, laboratory studies have shown that U_{max} for adult rainbow trout (tested with a similar acceleration of 0.08 cm·s^{-2}) is about 36% higher than the conventional U_{crit} (A.P. Farrell, and P. Bowering, Simon Fraser University, unpublished data), and reported U_{crit} values for mature sockeye salmon (*Oncorhynchus nerka*) at 18–20°C range from 1.5 to 2.3 BL·s^{-1} (Brett and Glass 1973; Jain et al. 1998; Farrell et al. 1998). Therefore, it is not unreasonable to predict that U_{max} capacity for coho salmon is around 3.08 BL·s^{-1} (i.e., 36% higher than the highest U_{crit} value of 2.3 BL·s^{-1}). Therefore, given that our highest U_{max} value was 2.96 BL·s^{-1}, we suggest that this speed represents the full U_{max} capacity for coho salmon in this type of swim test, and we have used this value to estimate to what extent and how quickly swimming performance was restored in

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other groups of fish. For example, 80% of vigorous coho salmon recovered 93% of the predicted U_{max} capacity within 20 min. A 1 h 20 min revival ensured that all vigorous fish swam at maximal capacity. Thus, in contrast to Paulik et al. (1957), who reported that adult coho salmon required several hours to recover swimming capacity after an initial exhaustive swimming bout, we suspect that adequate recovery of vigorous wild coho salmon can occur within minutes. Lethargic fish swam at 75% of predicted U_{max} capacity after 20 min revival, and at 86% of predicted U_{max} capacity after 1 h 20 min revival.

The swim-test results are important because they suggest that coho salmon, once appropriately revived, may have sufficient swimming capacity to avoid capture by nearby marine mammals, avoid recapture by fishers, and complete their spawning migration. However, while most vigorous and lethargic fish can swim rapidly after only a 20-min recovery period, we add the cautionary note that the fish were given a chance to increase their swimming speed slowly. Also, the conspicuously low U_{max} value for vigorous fish (67% of predicted U_{max} capacity) after netpen recovery suggests to us that revival for ≤10 min may not be sufficient (these fish did not have an additional 10-min recovery in the transporter box). Therefore, the swim tests have not directly addressed the issue of migration ability or avoidance behaviours. Consequently, future studies using tagged fish and tests of sprint performance would be particularly useful in resolving these issues.

We are left with a difficult decision regarding a recommendation as to when revived nontarget coho salmon should be returned to the ocean. Certainly a fixed recovery time period is inappropriate if fish are to be released at their peak of recovery. Therefore, we recommend that fish should be released when they first show signs of significant activity in the Fraser box; this would preclude the possibility of fish re-exhausting and stressing themselves further while trying to escape. Lethargic fish would benefit from a revival period of at least 20 min and ideally up to 1 h 20 min, at which time swimming performance might be nearly fully restored. Truly vigorous fish could be returned directly to the ocean, where they would complete their recovery in a natural environment.

Since vigorous fish swam well but were not fully recovered, it seems likely that full metabolic recovery is not a prerequisite for U_{max} swimming performance. A similar claim was made in earlier studies using repetitive U_{crit} tests (Jain et al. 1997, 1998; Farrell et al. 1998). We found that lethargic fish tended to recover more slowly and swim more slowly than vigorous fish. Our inability to statistically resolve such potentially important associations may go beyond the fact that the present study was performed under difficult field conditions and point to the fact that exhausted fish can recover their swimming performance more rapidly than we can reliably measure it. However, until we can get near-instantaneous, nonstressful muscle biopsies from exhausted fish, this issue will not be fully resolved.

Deliberate air exposure did not produce marked changes in the status of the lethargic coho salmon. In contrast, Ferguson and Tufts (1992) demonstrated that 60 s air exposure following an exhaustive swim by rainbow trout further increased plasma lactate levels and slowed recovery compared with fish that did not experience air exposure. The coho salmon in the present study were more exhausted at capture than the rainbow trout and this in itself may have limited the consequences of air exposure. However, it is worth noting that muscle glycogen levels tended to be lower in coho salmon after air exposure and this may explain the tendency towards slower recovery of muscle glycogen and ATP levels in fish in the Fraser box. Conversely, the trend towards higher PCr levels in air-exposed coho salmon at capture may simply reflect the fact that the fish were 2 min further into the recovery process than non-air-exposed lethargic fish. While the effects of air exposure were difficult to resolve, it was clear that lethargic fish suffered greater ionic and osmotic disturbances than vigorous fish. Whether this difference represents greater physical exertion prior to being hauled on board or simply a longer elapsed time since the fish fatigued in the gillnet is unclear.

Delayed mortality

As mentioned above, previous work with adult salmon showed that as many as 75% of captured fish can die within 24 h. In fact, Fisheries and Oceans Canada currently assesses commercial gillnet salmon fishers in British Columbia with a 60% mortality rate for coho salmon by-catch. Therefore, the present findings of no mortality among over 300 vigorous and lethargic coho salmon after 2 h revival in a Fraser box and only 2.3% coho mortality after 24 h revival in a netpen is a very encouraging improvement. The 24-h delayed mortality is similar to that reported in our previous study (2.4% mortality after 24 h; Farrell et al. 2000). An unresolved concern is the possibility that adult salmon, like non-salmonids (e.g., Olla et al. 1997), incur delayed mortality after 24 h. Consequently, further studies are needed to examine the longer term fate of revived coho salmon.

Previous studies have suggested that delayed mortality might be related to elevated plasma lactate levels and glycogen depletion (see Black 1958; Hochachka and Sinclair 1962; Wardle 1978), and that survival increases when this increase in plasma lactate is prevented. More recently, Milligan et al. (2000) showed that exhausted rainbow trout recovered faster if allowed to swim rather than remain stationary. This rapid recovery was also associated with low plasma lactate and cortisol levels. Similarly, mature coho salmon placed in a cage alongside a commercial troll vessel to recover while swimming slowly to keep pace with the vessel as it continued fishing activities also had lower plasma lactate and cortisol levels during recovery than those measured here, and showed no delayed mortality (A.P. Farrell, P.E. Gallaugher, and R. Routledge, Simon Fraser University, unpublished data). However, we observed a low rate of delayed mortality even though plasma lactate levels were >20 mmol·L^{-1}. Therefore, we suspect that the forced ventilation in the Fraser box promoted partial metabolic recovery, as well as recovery of swimming performance, and this was sufficient to largely prevent delayed mortality after 24 h. However, forced ventilation did not prevent the elevation in plasma lactate and cortisol levels, which may have long-term effects that still need to be investigated. Perhaps moderate swimming activity and low cortisol levels are key factors in preventing release of muscle lactate to the plasma and this may be of benefit in the longer term management of energy stores in skeletal muscle. At present, mechanistic ex-

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planations for the recovery of exhausted fish and delayed mortality remain incomplete.

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Summer movement and growth of juvenile anadromous salmonids in small western Washington streams

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Abstract: Movements of juvenile coho salmon (*Oncorhynchus kisutch*), cutthroat trout (*Oncorhynchus clarki clarki*), and steelhead trout (*Oncorhynchus mykiss*) were studied by observations and recapture of marked individuals in three western Washington streams to test the hypotheses that few fish would move, downstream movement would predominate, movers would be initially smaller and grow slower after movement than residents, and habitat quality would influence movement. Contrary to predictions, from 28 to 60% of marked fish moved at least one habitat unit, and immigration of unmarked fish also indicated considerable movement. Upstream movement predominated but the stream with the step-pool/cascade channel type had fewer upstream movers and greater distances moved downstream. Coho movers were not smaller than nonmovers, as predicted based on assumptions that movement results from competitive exclusion. Habitat units that coho left were smaller and shallower but lower in density than units where coho remained. Thus, movement is a common phenomenon rather than an aberration, and may reflect habitat choice rather than territorial eviction. Moreover, movers grew faster than nonmovers, so the "mobile fraction" of the population was not composed of competitively inferior fish but rather individuals that thrived. The phenomenon of small-scale habitat- and growth-related movements should be considered when planning and interpreting studies of juvenile salmonid ecology in streams.

Résumé : Les déplacements des juvéniles du Saumon coho (*Oncorhynchus kisutch*), de la Truite fardée (*Oncorhynchus clarki clarki*) et de la Truite arc-en-ciel (*Oncorhynchus mykiss*) anadrome ont pu être suivis grâce à l'observation et la recapture d'individus marqués dans trois cours d'eau de l'ouest du Washington afin d'éprouver les hypothèses selon lesquelles peu de poissons se déplacent, les mouvements vers l'aval prédominent, les poissons mobiles sont au départ plus petits et, une fois déplacés, ils croissent plus lentement que les poissons sédentaires et, finalement, la qualité de l'habitat influence les déplacements. Contrairement aux prédictions, de 28 à 60% des poissons marqués se sont déplacés d'au moins une unité d'habitat et l'immigration de poissons non-marqués reflétait l'existence de nombreux mouvements. Les déplacements vers l'amont prédominaient; cependant, dans le cours d'eau où il avait une succession de seuils et de fosses et des cascades, moins de poissons migraient vers l'amont et les distances parcourues vers l'aval étaient plus grandes. Les Saumons coho mobiles n'étaient pas plus petits que les sédentaires, contrairement aux prédictions qui assumaient que les déplacements étaient dus à l'exclusion par compétition. Les unités d'habitat abandonnées par les Saumons coho étaient plus petites et moins profondes que celles où les saumons restaient sur place et leur densité était moindre. Ainsi, les déplacements sont des phénomènes courants plutôt que des événements aberrants et ils reflètent peut-être un choix d'habitat plutôt que l'éviction d'un territoire. De plus, les poissons mobiles croissent plus rapidement que les sédentaires; la « fraction mobile » de la population ne se compose donc pas de poissons inférieurs face à la compétition, mais plutôt de poissons gagnants. Le phénomène des déplacements à petite échelle reliés à l'habitat et à la croissance doit être pris en considération dans la planification et l'interprétation d'études sur l'écologie de saumons juvéniles dans les cours d'eau.

[Traduit par la Rédaction]

Introduction

Movement is among the most important behavioral patterns of animals, as it allows them to respond to physical and biological conditions in their environment to increase their growth, survival and reproductive success. These movements occur over many scales of space and time, and may occur as individual responses to proximate conditions or as evolved responses by the population or species (Dingle 1996). Although some species undertake spectacular long-distance migrations, many animals move or disperse in a less directed and synchronized manner. These movements may be on eco-

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logically important spatial scales (e.g., a change in habitat) even though the absolute distance moved may not be great (Swingland and Greenwood 1984; Dingle 1996). Important questions regarding movement include the following: do most individuals move or only a few; do individuals move because they are in inadequate habitat or because they cannot compete in high-quality habitat, and; what are the fitness consequences of movement?

The empirical study of animal movement often depends on documenting the distribution of animals of known origin. Typically, this is done by marking and later searching for individuals within a defined study area. Animals that move are less likely to be detected than those that do not (Koenig et al. 1996), and this leads to biased (under)estimates of movement and tends to lead to the neglect of the possible fitness benefits of movement. Owing to the importance of salmonid fishes (genera *Oncorhynchus*, *Salmo*, and *Salvelinus*) in recreational and commercial fisheries and as components of regional biodiversity, extensive research has been conducted on their movements. Because of this extensive research, salmonids provide a good opportunity to test hypotheses about movement. These fishes display classic migrations, the exodus of juveniles (smolts) to the ocean (Iwata 1995) and return of maturing adults to their natal stream (Dittman and Quinn 1996), as well as exhibiting dispersal movements of juveniles in freshwater (reviewed by McCormick et al. 1998).

Studies of the habitat use and movement patterns of juvenile anadromous salmonids in coastal North American streams have indicated two major movement events prior to seaward migration: the dispersal of fry following emergence in the spring and early summer and the movement of parr to low-velocity or off-channel rearing areas in the fall and winter. Research in coastal systems has generally concentrated on the spring or (especially) fall periods, and information on the movements of juvenile anadromous salmonids during the summer, following their initial dispersal but prior to their fall redistribution, is sparse. Studies have indicated that few juveniles move during summer relative to the numbers moving during the spring dispersal and fall redistribution events (e.g., Hartman and Brown 1987). These patterns are best documented in coho salmon (*Oncorhynchus kisutch*), the most abundant juvenile salmonid in most coastal streams accessible to anadromous fishes. This species typically spends one full year in freshwater (or more in the northern end of its range) prior to seaward migration and tends to occupy pool habitats (Sandercock 1991).

Unlike the studies on coastal populations, recent studies of age-1+ and older salmonids in small, high-elevation streams subject to continental climate regimes have shown considerable movement in summer (Gowan and Fausch 1996; Young 1996). This is in contrast to the "restricted movement paradigm" (RMP) that has been generally accepted within the fisheries community (Gowan et al. 1994). The RMP holds that salmonids in streams generally occupy small home ranges that they seldom leave. Gowan et al. (1994) challenged the RMP and asserted that many studies claiming to support the RMP were unlikely to detect movement and often made claims of limited fish movement based on the recapture of only a small fraction of marked individuals. Studies designed under the assumption that fish are likely to move have often yielded results that contradict the RMP (e.g., Young 1996). Differences in observed movement among salmonid populations may be attributable to differences in the designs and techniques of respective studies (Young 1996) and to intrinsic differences in the habitats or ecology of the fishes. One may expect less upstream movement in high-gradient streams, for example, but many studies of movement do not report gradient. Despite strong evidence against the RMP from continental populations of salmonids, there is a lack of evidence against restricted summer movement in coastal populations of juvenile anadromous salmonids.

Movement of juvenile anadromous salmonids prior to seaward migration is generally believed to be a response to poor or declining habitat conditions, evidenced by a negative relationship between pool area and movement (Bilby and Bisson 1987). Fish may move in response to interrelated factors including aggressive interactions (Chapman 1962), changes in discharge or temperature (Bjornn 1971), or decreasing food abundance (Wilzbach 1985). Declining stream discharge shrinks available habitat, increasing density. The incidence of agonistic behavior increases with density (to a point) and competitively inferior fish may move downstream (Chapman 1962; Titus 1990).

To the extent that movement is a response to saturated habitat, individuals that move are expected to be smaller and grow slower than fish that do not move. Smaller individuals are competitively inferior, and prior residency provides a competitive advantage (e.g., coho salmon, Rhodes and Quinn 1998; steelhead trout, *Oncorhynchus mykiss*, Abbott et al. 1985). A small fish that loses a competitive interaction and moves to another habitat may encounter prior residents and be forced to accept marginal habitat or continue moving. Alternatively, individuals may leave low-density, poor-quality habitat and encounter unoccupied high-quality habitat, where they experience high growth rates, which could increase survival at subsequent life stages (Quinn and Peterson 1996). However, the fate of salmonids that move is seldom known. Accordingly, we investigated the summer movements of individually marked anadromous, age-0+ coho salmon, and age-0+ and 1+ cutthroat (*Oncorhynchus clarki clarki*) and steelhead trout in three coastal streams of Washington State, U.S.A., and tested the following hypotheses: (*i*) mobile fish within a population represent a small minority; (*ii*) movement is predominantly downstream; (*iii*) mobile fish are initially smaller than sedentary fish; (*iv*) mobile fish grow more slowly than sedentary fish, and; (*v*) fish more often move away from low-quality than high-quality habitat.

Materials and methods

Study sites

Big Beef Creek (BBC), studied in 1997 and 1998, flows into the east side of Hood Canal, Wash. At the study section, about 1 km above tidewater, the bankfull width was approximately 15 m, and the gradient was 0.8% (Table 1). The channel type was forced pool-riffle (channel classifications from Montgomery and Buffington 1997) with a gravel and cobble substrate. The study area was logged approximately 100 years ago, and the riparian vegetation is now predominantly deciduous, with second-growth conifers also present. The riparian canopy provides incomplete coverage of the broad, aggrading channel, with bank vegetation providing limited overhead cover for fish. Discharge during the summer study

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Table 1. Stream characteristics.

Stream characteristic	Big Beef Creek	Shuwah Creek	East Fork Griffin Creek
Gradient	0.8%	2%	5.7%
Bankfull width (m)	15	6.5	5.5
Habitat unit length (m)	15.7	6.9	3.8
Channel classification	Forced pool-riffle	Forced pool-riffle	Step-pool/cascade
Max. discharge (1998 study) ($m^3 \cdot s^{-1}$)	0.27	0.09	0.1
Density (salmonids$\cdot m^{-2}$)	0.22 (1997) 0.87 (1998)	0.33	0.31
Pool area	75% (1997) 61% (1998)	55%	54%
Riffle area	25% (1997) 39% (1998)	36%	46%

Note: Gradient, Bankfull width, and Mean density are the means for each study section. Habitat unit length is the average length of habitat units in each study section. Channel classification from Montgomery and Buffington (1997). Max. discharge is the maximum discharge (estimated for Shuwah Creek and East Fork Griffin Creek; U.S. Geological Survey data for Big Beef Creek) during the 1998 study period, which was the period between fish marking and recapture. Pool area and Riffle area are the percentages of the total area of each study section. "Riffle" includes cascades. Glides were not included.

periods ranged from 0.27 to 0.16 $m^3 \cdot s^{-1}$ in 1997 and from 0.26 to 0.10 $m^3 \cdot s^{-1}$ in 1998.

In 1998, Griffin Creek and Shuwah Creek were also studied. Griffin Creek is a tributary of the Snoqualmie River, which flows into central Puget Sound. The study section was located on the East Fork of Griffin Creek, in a high-gradient (5.7%) confined reach, with 5.5-m average bankfull width and angular boulder and cobble substrate (see Table 1). This study section was the highest-gradient channel located that was utilized by coho salmon and also satisfied our other stream-selection criteria. The upper and lower ends of the section were step-pool channels and the steeper middle part of the section was a cascade channel. Stream discharge during the summer ranged from 0.10 $m^3 \cdot s^{-1}$ to near zero when the lower portions of the study section went dry in late August. The riparian zone was well shaded by second-growth conifers with deciduous streambank vegetation. Large wood was sparse within the wetted channel and streambank vegetation provided little overhead cover; prey refuge habitat consisted primarily of interstitial spaces between substrate elements.

Shuwah Creek is a tributary of the Soleduc River near Forks, Clallam County, Wash. Bankfull width of the study section was 6.5 m and the incising, moderately confined channel was forced pool-riffle type with gravel and cobble substrate (see Table 1). Summer discharge ranged from 0.09 $m^3 \cdot s^{-1}$ to near zero when the lower portion of the study section ceased flowing in early September. Vegetation within the study section consisted of second-growth conifers, with dense overhanging salmonberry (*Rubus spectabilis*) on the banks. Abundant large wood, undercut banks, and overhanging vegetation provided prey refuge habitat.

These three streams were selected because they represented a range of channel types and gradients, and had the same salmonid species. All three streams contained age-0+ coho salmon, and age-0+ and 1+ steelhead and cutthroat trout. Given the close proximity of the study streams to marine waters and the length-frequency distributions of captured fish, all salmonids were assumed to be anadromous. No age-2+ steelhead were observed in any stream, and few age-2+ cutthroat trout were observed: one each year in BBC, four in Shuwah Creek, and none in Griffin Creek. Common predators in the three streams included sculpins (*Cottus* spp.), belted kingfishers (*Megaceryle alcyon*), great blue herons (*Ardea herodius*), river otters (*Lutra canadensis*), and raccoons (*Procyon lotor*).

The study streams are all subjected to a maritime climate regime characterized by mild wet winters and summer drought. All of the streams are below elevations that have continuous winter snow; precipitation falls almost entirely as rain in the study subbasins. In contrast with streams under continental climate regimes, maximum discharge events typically occur between November and March in the study streams.

Study design

The basic study design in all three streams was to capture all salmonids within a defined study section, measure and individually mark each fish, follow their movements throughout the summer using periodic snorkel surveys, and recapture individuals in the fall to obtain final measurements. Habitat units where fish were captured were measured (slope, area, and residual depth) and classified as riffles, pools, glides, or cascades. Movement could thus be related to species, initial size, growth rate, density, and habitat features. We marked fish using the photonic marking system developed by NEWWEST Technologies, Santa Rosa, Calif. This system consists of a modified mass-inoculation gun powered by compressed CO_2, which injects marking fluid composed of pigmented latex microspheres suspended in deionized water (with the appearance of low-viscosity paint). Fish were marked in the dorsal fin, upper and lower lobes of the caudal fin, and anal fin. With this method, hundreds of individuals could be uniquely identified with marks discernable to a snorkeler (Kahler 1999). Although not specifically tested, no behavioral differences between marked and unmarked individuals were observed.

We collected and marked salmonids in BBC between 25 July and 6 August 1997. Blocking nets were placed at both ends of each habitat unit and fish were captured with pole seines using three-pass removal. The pole seines were seine nets of various dimensions with mesh sizes of approximately 3 mm, with 1.8-m long wood dowels attached at each end to facilitate maneuvering of the net. Captured fish were anesthetized with MS-222, identified as coho or trout, measured to the nearest millimeter (fork length) and weighed to the nearest 0.1 g. Salmonids 45 mm and larger were individually marked and all fish were returned to the habitat unit where they were captured. We conducted snorkel surveys on 15 and 22 August, 4 and 7 September, and 22 October 1997 to locate marked individuals by habitat unit. In addition, on 26–29 August and 21–23 September, fish within the study section were sampled using pole seines, identified, measured, weighed, and released into the habitat unit where they were recaptured.

In addition to the snorkeling, in July 1997 we bounded a 331-m study section of BBC with weirs with two-way fish traps to intercept all fish moving into and from the study section. Weirs were V-shaped, and constructed of 0.9 × 2.4 m wood-frame panels of 6-mm mesh hardware cloth, with the "V" opening upstream. At the

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apex of the "V," a 10-cm diameter ABS (acrylonitrile-butadiene-styrene) pipe conveyed fish downstream into a trap. The Washington Department of Fish and Wildlife (WDFW) required that water velocity at the screens be minimized to prevent impingement of juvenile fish, so a dam was constructed downstream of the screens. Fish moving upstream were directed into an upstream trap at a notched opening on the dam. We checked the traps daily, usually morning and evening, from 21 July until 16 September 1997, when a freshet destroyed the weirs. Fish in the traps were measured and identified, checked for marks, and released in the direction that they were traveling. Starting on 1 August 1997, fish entering the study section were given right or left pelvic fin clips (following Gowan and Fausch 1996) designating their direction of movement.

In 1998, we repeated the snorkeling study on BBC but the addition of similar marking and snorkeling on Griffin and Shuwah creeks precluded operation of the weir and traps on BBC. We made no recapture efforts until the end of the study in 1998, and we extended snorkel surveys upstream and downstream of the study sections to account for fish that had moved beyond section boundaries, in part to compensate for the lack of trapping.

On BBC in 1998, the study section (where fish were marked) was 184 m with the downstream end in the approximate location of the 1997 downstream weir. We began fish collection and marking on 15 June 1998 using the same methods as in 1997, except that trout older than age-0+ were identified to species. We measured and numbered habitat units in the study section and in two sections extending 163 m upstream of and 230 m downstream of the study section. We conducted weekly snorkel surveys of all sections (577 m) from 7 July to 15 September 1998, and recaptured fish from 16–18 September 1998 in the study section and all other units where marked fish were observed on 15 September.

In Griffin Creek, we collected fish for marking in a 119-m-long study section on 23–24 June 1998, following the same procedures as in BBC in 1998 except that three-pass electrofishing was used rather than pole seining. We measured and numbered habitat units in the study section and for 32 m upstream, and 111 m downstream of the study section. We had cataloged habitat units over 100 m upstream of the study section, but beyond 32 m, a cascade dewatered within three weeks, isolating upstream units. We conducted weekly snorkel surveys of the study, and upstream and downstream sections (262 m) from 16 July to 19 August 1998 when the study section consisted of mostly isolated pools with a few habitat units still connected by flowing water. We recaptured fish on 21 August 1998 via electrofishing starting 111 m downstream of the study section, and continuing to the upstream end of the study section. The stream was dry upstream of the study section for hundreds of meters and had been since early August.

On Shuwah Creek, we divided a 301-m study section into three subsections: a 98-m downstream subsection and an 84-m upstream subsection where fish were marked, and an intervening 119-m subsection where no fish were marked. The study section was configured in this manner to accommodate the design of a concurrent companion study. We collected fish within the upstream and downstream subsections for marking on 1–3 July 1998, using three-pass electrofishing as in Griffin Creek. We numbered and measured habitat units within the study section, and 120 m upstream and 178 m downstream of the study section. We conducted weekly snorkel surveys of all sections (599-m total) from 14 July to 31 August 1998 and recaptured fish on 6–8 September 1998 in the study section and all other units where marked fish were previously observed.

We would have preferred to use electrofishing in all streams but WDFW would not permit electrofishing in BBC. Fortunately, BBC was well suited for seining; most of the habitat units were large and structurally simple. The large pools that had complex features such as woody debris jams would have proven challenging for electrofishing, considering the large volume of water and complexity of escape cover. Both coho salmon and cutthroat trout were easily collected by seining because of their tendency to forage high in the water column of pools. Steelhead were also readily captured in BBC and were a larger fraction of the total catch there than in the other streams.

Wiley and Tsai (1983) compared electrofishing and seining in small streams and concluded that the "…electroshocker was more effective than seines for making quantitative collections." However, we were not conducting population estimates but collecting fish for marking, and made inferences only on fish recaptured or observed by a snorkeler. Presumably, marked fish would be equally observable by a snorkeler, regardless of initial capture method at marking. Seining undoubtedly affected recapture efficiency in BBC but would not have introduced a bias toward the capture of either movement class (as defined below). While it is possible that sampling technique could have introduced some behavioral artifact, there were other differences among streams that also could have done so. Any bias towards density resulting from differences in capture technique could not be determined; both the lowest density (1997) and the highest density (1998) observed during the study were in BBC. Such a possible bias was considered by the inclusion of "stream" as a variable in statistical analyses.

For data analysis, we classified all marked fish either observed during snorkel surveys or recaptured as "recovered". We called fish recovered in a habitat unit other than where they had been marked or previously located "movers". We called fish that were recovered in their original habitat unit "nonmovers". The term nonmovers was not intended to imply that fish had not moved, only that we had not detected their movements. Both weekly snorkeling and final recapture efforts were during daylight hours, thus we would have failed to detect movements occurring on a smaller time scale, such as the diel changes in habitat use reported by (Hilderbrand and Kershner 2000).

We calculated the specific growth rates (μ: ln(mm)·day^{-1}) of recaptured individuals in each stream from Ricker (1979)

$$\mu = (\ln L_1 - \ln L_0)/\Delta t$$

where L_1 is the final length (mm) recorded at recapture, and L_0 is the initial length (mm) recorded at marking, and Δt is the growth period in days between marking and recapture.

We selected as surrogates of habitat quality two physical variables, residual depth and area, and one biological variable, salmonid density, to determine whether habitat influenced fish movement or growth. We selected density as a variable because it provides a measurable indicator of the intangible factor competition. We defined residual depth as the maximum depth of a habitat unit, minus the maximum depth at the hydraulic control (the downstream streambed feature that creates the lip of the pool) of that unit. We calculated area by multiplying the unit's length by its average width. We defined density as the number of salmonids (all species) per unit area at the time of marking. For comparison, higher-quality habitat units would have greater area and residual depth and lower density (less competition) than lower-quality habitat units. We used the number of habitat units traversed by a mover for analysis of movement distances because the differences in channel types, sizes, and gradient made it inappropriate to compare the number of meters moved by individuals in the three streams. For example, because of the among-stream differences in size of habitat units, a fish could move 10 m in BBC without leaving its habitat unit whereas a fish might traverse 2–3 habitat units with a 10-m movement in Griffin Creek. Thus, a measure of the number of habitat units traversed provided a more ecologically meaningful comparison among streams than did the number of meters moved.

Multiple observations provided chronological records of movement as well as initial and final location. However, some individuals moved both upstream and downstream during the study, making their categorization as either upstream or downstream movers ambiguous, especially if they returned to and were finally recaptured

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Table 2. Numbers of marked fish, recovered fish (i.e., recaptured or snorkel observation), and movers (i.e., fish observed to have moved at least one habitat unit from where they were marked) in each stream by species.

Salmonids	BBC 1997	BBC 1998	Griffin	Shuwah
Marked				
Total	707	501	107	141
Coho	231	434	82	67
Cutthroat	31	12	22	47
Steelhead		39	2	9
Trout fry	445	16	1	18
Recovered				
Total	247	104	55	101
Coho	99	87	44	59
Cutthroat	10	3	11	24
Steelhead		13	0	6
Trout fry	138	1	0	12
Movers				
Total	115	29	33	55
Coho	40	24	26	29
Cutthroat	4	2	7	15
Steelhead		3	0	3
Trout fry	71	0	0	8

Note: Trout fry were age-0+ trout that were not identified to species. Cutthroat and steelhead trout were age-1+ and age-2+ (six total in all streams), and were not differentiated in BBC during 1997. BBC = Big Beef Creek.

at their original marking location. Accordingly, we used a count of the total number of upstream and downstream movement events by all fish in each stream to indicate directional movement patterns. Analysis using each movement event treats repeated movements by individuals as independent, which they are not, although they took place from different habitat units and were separated by significant periods of time. Therefore, statistical analyses using the number of movement events were repeated using the number of moving individuals, and results of both tests are noted.

Although marked steelhead and cutthroat trout were recovered in all streams, sample sizes, species, and age composition of trout varied greatly among streams. Because salmonids differ in habitat use among species and age groups (e.g., Bisson et al. 1988), we conducted most analyses using only coho salmon data with the exception that "density" always refers to the number of salmonids (all species) per square meter. Throughout the paper, we will indicate when results or discussions apply to all salmonid species or to only coho.

We used χ^2 tests to compare proportions of movers and nonmovers, and direction of movement within and among streams. We used an analysis of variance (ANOVA) blocked by stream to compare differences in length and growth rate between movers and nonmovers, and between upstream and downstream movers. We used Tukey multiple comparisons for post-hoc analyses of ANOVA and χ^2 tests. We used logistic regression to examine the relationship between movement and habitat characteristics. For all tests, we considered $P \leq 0.05$ indicative of significance.

Results

In 1997, 707 juvenile salmonids were individually marked in BBC, and 749 juvenile salmonids were marked in Big Beef, Griffin, and Shuwah creeks combined in 1998 (Table 2). Location data were collected on 247 (35% of marked) fish in 1997 and 260 (35% of marked) fish in 1998. We rejected the hypothesis that mobile fish within the population represented a small minority. Movers (all species) comprised 47% of the recovered fish in 1997 and 28–60% of the recovered fish in 1998, depending on the stream (Fig. 1), and 14–36% of the movers moved more than once (Table 3).

More upstream than downstream movements (included coho salmon and trout) were recorded in almost all cases (BBC 1997, 51%; BBC 1998, 72%; Shuwah, 59%; Griffin, 45%), although only in BBC in 1998 did the numbers of upstream and downstream movements differ significantly from a 50:50 ratio (χ^2 test; $P < 0.01$). Similar results (BBC 1997, 53%; BBC 1998, 89%; Shuwah, 63%; Griffin, 45%) were obtained using net displacement data (i.e., comparing final recapture location to marking location, ignoring intervening movements). Further analyses were conducted using only coho salmon data, with the exception that "density" always refers to the number of salmonids (all species) per square meter.

The initial lengths of coho salmon differed among streams but the initial lengths of movers and nonmovers did not significantly differ within streams ($P = 0.808$; Table 4). Within-stream differences in mean initial lengths of upstream and downstream movers were not significant ($P = 0.628$), but movers grew faster than did nonmovers ($P = 0.031$; see Table 4).

The mean distances (measured in habitat units) moved upstream by coho salmon were similar to the downstream distances in all streams except Griffin Creek, where they moved over four times farther downstream than upstream ($P < 0.001$; Table 5). Post-hoc multiple comparisons (Tukey Honestly Significant Difference) indicated that the mean distance in Griffin Creek differed from the mean distances in BBC in 1997 and 1998, and Shuwah Creek ($P = 0.006$, $P < 0.001$, $P = 0.001$, respectively), but distances moved in BBC and Shuwah did not differ from each other. The proportions of upstream and downstream movements by coho salmon differed among streams (χ^2 test; $P < 0.005$, see Table 5). The lowest proportion of upstream movement was observed in Griffin Creek (45%) and the highest proportion was in BBC (56% in 1997 and 68% in 1998), but this overlapped with Shuwah Creek (56%).

We used multiple logistic regression to evaluate the relative roles of physical habitat and density on the likelihood of movement by coho salmon. Our initial analysis included coho that did not move and all movement events by those that moved, for a total of 317 complete observations. The habitats from which fish moved were smaller in area (59.4 m^2 vs. 95.2 m^2; $p = 0.029$) and depth (0.50 m vs. 0.64 m; $p = 0.007$) than those where the fish stayed (see Table 4). Paradoxically, the habitats from which fish moved had lower densities (0.57 fish·m^{-2} vs. 0.73 fish·m^{-2}; $p = 0.002$) than the habitats where they remained, thus the fish tended to leave small habitat units despite lower densities. Stream was entered into the model as a "dummy variable", but was not significant ($p = 0.71$), indicating that the patterns were consistent among sites. Because of our concern for the violation of the data-independence assumption when using movement events as the dependent variable (noted above), the logistic regression was repeated using only the first move by each fish (ignoring subsequent moves by those individuals). This reduced the sample to 268 individuals but

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Fig. 1. The percentages of recovered juvenile salmonids and movers in Big Beef Creek in 1997 and 1998 (BBC 1997 and BBC 1998) and Griffin and Shuwah creeks in 1998. The pie charts on the left show the total number of marked fish (*N*) in each creek. "Missing" is the percentage of marked fish not recovered; "Recovered" fish were either observed by a snorkel survey or captured. The charts on the right show the proportions of recovered fish that moved at least one habitat unit from where they were marked (Movers) and that remained in the original unit (Nonmovers).

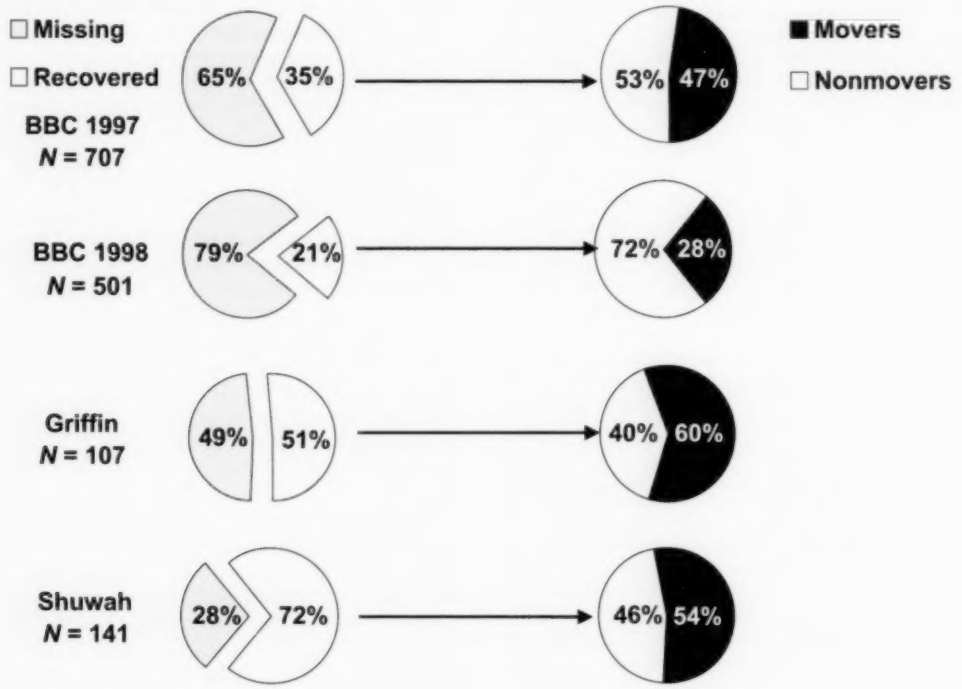

Table 3. The numbers (and percent, in parentheses) of fish moving one or more times per summer in Big Beef Creek (BBC), Griffin Creek, and Shuwah Creek.

Creek/year	1 move (%)	2 moves (%)	3 moves (%)	4 moves (%)	Movements-to-fish ratio
BBC/1997	79 (77)	22 (21)	2 (2)	0	1.25
BBC/1998	25 (86)	2 (7)	2 (7)	0	1.21
Griffin/1998	27 (82)	4 (12)	2 (6)	0	1.24
Shuwah/1998	35 (64)	16 (29)	3 (5)	1 (2)	1.45

Note: The movements-to-fish ratio represents the number of movement events observed in each creek divided by total number of individual fish that moved.

produced broadly similar results. There were significant effects of depth (0.51 m vs. 0.65 m for fish that moved and stayed, $p = 0.004$) and density ($p = 0.026$), but not area ($p = 0.086$) or stream ($p = 0.58$).

Discussion

Percentages of mobile fish within the populations

Rather than being a small minority within the populations, movers represented from 28 to 60% of the recovered fish within the study streams and 14 to 36% of them moved more than once. Thus, movement from one habitat unit to another represented common behavior for these salmonid populations. Further evidence for the prevalence of movement, albeit indirect, comes from the incidence of unmarked fish in the study sections of Griffin and Shuwah creeks. The number of unmarked fish in the study sections increased from 23 following marking to 203 at recapture in Shuwah Creek and from 7 to 62 in Griffin Creek, despite the fact that 18 of the 31 habitat units were either dry or devoid of fish at the time of recapture in Griffin Creek. This nearly ninefold increase in unmarked fish due to immigration indicated highly mobile fish populations.

In all streams, the number of marked fish observed declined over time, especially in BBC in 1998. One possible explanation for this decline is loss of marks. Mark quality was variable and in some cases declined over time eventually becoming unreadable. However, usually only one or two of the four marks faded and even when the colors became indistinguishable, it was obvious that the fish had been marked.

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Table 4. Coho salmon initial lengths (mm) of nonmovers and movers and of upstream and downstream movers; growth (ln mm·day^{-1}) of nonmovers and movers; mean density (salmonids·m^{-2}), residual depth (cm), and area (m^2) of habitat units from which coho moved or remained.

Comparison	BBC 1997	BBC 1998	Griffin	Shuwah
Initial length				
Nonmovers	71 (6.7) [59]	58 (7.6) [63]	58 (8.0) [18]	68 (12.3) [30]
Movers	70 (5.9) [34]	59 (6.4) [24]	60 (8.3) [26]	66 (13.1) [29]
Upstream	69 (6.2) [20]	60 (5.8) [21]	60 (10.1) [14]	67 (14.2) [23]
Downstream	72 (4.4) [16]	61 (6.9) [10]	59 (6.9) [17]	67 (14.5) [18]
Growth ($\times 10^{-3}$)				
Nonmovers	2.01 (0.97) [9]	Insufficient data	0.91 (0.74) [8]	1.36 (0.75) [15]
Movers	2.90 (1.06) [19]		1.35 (0.63) [4]	1.96 (1.25) [15]
Mean density				
Nonmovers	0.42 (0.21) [59]	1.19 (0.43) [65]	0.65 (0.19) [22]	0.38 (0.11) [29]
Movers	0.42 (0.23) [36]	1.12 (0.49) [30]	0.50 (0.27) [33]	0.39 (0.16) [50]
Habitat depth				
Nonmovers	78 (3.1) [59]	67 (1.5) [65]	23 (0.5) [21]	59 (2.3) [29]
Movers	66 (3.6) [35]	53 (2.0) [30]	21 (0.6) [29]	54 (2.0) [50]
Habitat area				
Nonmovers	160 (100) [59]	88 (49) [65]	20 (5) [18]	36 (16) [29]
Movers	131 (74) [36]	61 (36) [30]	16 (7) [34]	36 (17) [50]

Note: Parentheses indicate standard deviations; brackets indicate sample sizes.

Table 5. Mean upstream and downstream distances (measured in number of habitat units and in meters) moved by coho salmon movers in each stream (standard deviations in parentheses), maximum distances moved in each direction, and the proportions of movements that were upstream, expressed as the percentage of all coho salmon movements from the point of capture or previous observation.

Comparison	BBC 1997	BBC 1998	Griffin	Shuwah
Distance upstream				
Units moved	3.6 (3.6)	4.4 (3.6)	2.5 (2.8)	6.4 (7.9)
Meters moved	46.5 (10.9)	42.8 (8.2)	9.8 (9.6)	42.2 (14.2)
Maximum (m)	234	125	39	213
Distance downstream				
Units moved	5.8 (6.7)	3.0 (3.0)	11.0 (14.1)	5.2 (5.6)
Meters moved	50.5 (15.3)	21.6 (3.3)	43.4 (57.4)	26.3 (5.6)
Maximum (m)	178	142	201.5	163
Proportion upstream	56%	68%	45%	56%

Note: BBC = Big Beef Creek.

Thus, a recovered fish with an illegible mark was counted as a marked fish, although no analysis on individual attributes was possible. We therefore discount mark loss as an explanation for the decline in marked fish.

Two other factors that might contribute to the decline of marked fish over time are emigration and mortality. The weirs on BBC in 1997 indicated that only 1% (7 fish) of the marked fish moved from the study section. Despite this low number of emigrants from the study section and frequent sampling, only 29% of the marked fish were recaptured at the end of the study, and an additional 4% were confirmed mortalities over the course of the summer. Allowing for some capture inefficiency, this would indicate that the fish population in BBC in 1997 experienced a mortality rate generally consistent with rates estimated (49%; Nickelson et al. 1993) for coho salmon elsewhere. A high mortality rate has been cited as evidence for limited movement in cases where only a few marked fish were recovered (see discussion in Gowan et al. 1994). In the present study, the decline in marked fish over time appears to have resulted from a combination of high mortality with substantial small-scale but limited large-scale movement.

Direction of fish movement

The prediction that summer movement would be predominantly downstream originated from observations that aggressive interactions force competitively inferior members of a coho salmon population of to emigrate (e.g., Chapman 1962), and that the directional nature of streams might cause displaced individuals to move downstream. This hypothesis was summarized by Titus (1990) as follows: Large, dominant fish with high growth potential have territories that expand as they grow, and these dominant fish force smaller fish with lower growth potential to move downstream.

Support for the expectation of downstream movement by age-0+ anadromous salmonids can be found in the literature for coho salmon (Hartman et al. 1982) and chinook salmon (Bradford and Taylor 1997). However, this contrasts with the

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predominance of summer upstream movement in populations of age-1+ and older salmonids in the Rocky Mountains (Gowan and Fausch 1996) and brook trout (*Salmo fontinalis*) in Idaho (Adams et al. 2000). In the present study, movements were not predominantly downstream. More movements were upstream than downstream in all streams except Griffin Creek, where 45% of the movements were upstream.

Previous studies (e.g., Peterson 1982) also reported that juvenile coho and cutthroat moved upstream but they provided only counts of the number moving through traps over a given period, not proportions of the population. We were able to consider the total number of observed movement events by all fish in each stream rather than the numbers of mobile fish (movers) because the frequent snorkeling observations allowed multiple observations per fish. For example, had only marking and final recapture data been considered (ignoring intervening movements detected by snorkeling), we would have missed 36% of the movement in Shuwah Creek. However, analysis of our data using only marking and final recapture locations (i.e., one data point per fish) supported similar conclusions to those based on all movement events; there was more movement upstream than downstream in all streams except Griffin Creek (45% upstream).

While many fish in our study streams moved once in only one direction, some moved more than once and in both directions and several returned to their original marking location. The complex movement patterns we observed suggested that juvenile salmonids may engage in "exploratory" movement behavior as discussed by Smithson and Johnston (1999) for non-salmonids in Little Glazypeau Creek, Ark. Similarly, Armstrong et al. (1997) reported that Atlantic salmon parr showed three behavior patterns in an experimental stream: some settled immediately and did not move, some explored the available habitat extensively and then settled, and some never settled but moved throughout the stream section.

Fish size, movement, growth, and habitat quality

The hypothesis that coho salmon movers would be initially smaller than sedentary fish was based upon the assumption that movement would result primarily from size-biased competitive interactions (Chapman 1962; Rhodes and Quinn 1998), but our results did not support this hypothesis. Movers were also expected to grow slower than sedentary fish under the assumption that movers would be intruding into territories held by others and so would have a competitive disadvantage (Rhodes and Quinn 1998) but the movers grew faster than nonmovers. Perhaps competitive interactions were not the primary motivation for summer movement in our study streams.

We examined the movements of age-0+ coho salmon, whereas the studies that formed the basis for the hypotheses concerning size and growth examined aggressive interactions or foraging behavior and growth. For example, Nielsen's (1992) observations of coho salmon foraging behavior and growth were based primarily on fish that remained in their original habitat unit but 40–73% of the marked fish left their original habitat unit. Nielsen (1992) compared the growth rates of individuals classified as dominant and subdominant, and a third class ("floaters") of fish that were not associated with dominance hierarchies. The growth rate of coho salmon that left the study sections was unknown, so it would be inappropriate to compare the movers in our study with the "floaters" in Nielsen's (1992) study.

Comparison of the physical habitat features and level of competition in units where fish stayed and where they departed yielded important results. Coho salmon movement seemed to be motivated primarily by habitat size and especially depth. This is consistent with the preference of the species for pools (e.g., Bisson et al. 1988), with experimental evidence that probability of mortality was related to habitat complexity and depth when area was controlled for (Lonzarich and Quinn 1995), and with higher mortality rates in riffles than in pools (Kruzic et al. 2001). Depth may confer greater protection from avian predation than area, though deep pools may also be more suitable for predatory fishes such as larger salmonids (although few trout greater than age-1+ were observed).

The habitat units that coho left actually had lower densities than the units where they remained, in contrast with the assumption that movement takes place as a result of competition for space. Combined with the evidence that the coho that moved were similar in size to those that remained, this indicates that movement was more a matter of habitat selection than displacement. It seems that coho salmon in high-quality habitats (in our case deep, but other attributes may also be important) tend to remain there despite comparatively high densities. Indeed, the higher density may be a consequence of reluctance to leave. These habitats may afford protection at the expense of growing conditions, as growth is density dependent (e.g., Roni and Quinn 2001). Fish in small, shallow habitats tend to leave despite the fact that (or resulting in the fact that) densities in such habitats are low. Fish in small, shallow habitats may be the first to experience the inadequacies of their habitats as their body size increases, and this would be especially true of the fastest-growing fish in the smallest, shallowest habitats. Such movement by fish that outgrew their habitat was reported by Forseth et al. (1999) for older juvenile brown trout (*Salmo trutta*). Fish that moved encountered suitable habitat and grew faster than individuals that remained. However, it remains unclear whether the faster growth rates of movers were attributable to some superiority of the habitat to which they moved, or to an inherently faster growth rate possessed by those fish. The lack of significant differences in the initial lengths of movers and nonmovers suggests that movers encountered superior foraging opportunities.

Stream characteristics and movement

Both upstream and downstream distances moved (in terms of habitat units) were similar in all streams except Griffin Creek, where coho salmon moved farther downstream and shorter distances upstream than in the other streams. Shuwah Creek and BBC are both forced pool-riffle channels with gradients of 2% or less, whereas Griffin Creek is a relatively high-gradient (5.7%) step-pool/cascade channel. Thus, extensive upstream movement in Griffin Creek would have been more difficult than in BBC or Shuwah Creek. A more extensive study design, including a range of gradients, would be needed to test the hypothesis that juvenile coho salmon movements are affected by gradient per se. However, the step-pool and cascade channel types characteristic of higher gradients are less extensively used by coho salmon than the

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pool-riffle and plane bed channels found at lower gradients (Montgomery et al. 1999), making such a comparative study difficult.

Unlike the other streams, the number of downstream movement events by coho salmon exceeded upstream movement events in Griffin Creek. Several hundred meters of Griffin Creek upstream of the study section went dry by the 10 August 1998 snorkel survey, precluding further upstream movement. Fish may have moved downstream to avoid dewatering, as Hubble (1992) noted for age-0+ steelhead in intermittent tributaries to Satus Creek, Wash. Dewatering also occurred in Shuwah Creek but started from the downstream end, and only affected the lower sixth of the study section.

Both Griffin and Shuwah Creeks have similar bankfull widths and discharges, and portions of each became intermittent. These similarities in flow regime probably explain the greater proportions of salmonids moving in these streams than in BBC, despite the differences in channel type and gradient. The rapid loss of suitable habitat in Shuwah and Griffin Creeks as flow declined resulted in increased fish mobility. The flow in Griffin Creek declined earlier and more drastically than in Shuwah Creek and even more fish moved in Griffin Creek than in Shuwah Creek.

Downstream movement may have additional adaptive significance (beyond the avoidance of dewatered sections) in the east fork of Griffin Creek because of the distribution of high-quality rearing habitat in the Griffin Creek system. The majority of high-quality rearing habitat for coho salmon occurs downstream from the study section on East Fork Griffin Creek, in the form of large in-channel wetlands on the main stem of Griffin Creek. Quinn and Peterson (1996) reported increased overwinter survival and larger smolt size by coho salmon rearing in headwater wetlands on BBC. Perhaps downstream movement produces similar advantages for coho in Griffin Creek as well.

In conclusion, we observed that small-scale movement (i.e., several habitat units) and especially upstream movement was common in three streams. The direction of movement was influenced by channel type and (or) gradient (steeper-gradient step-pool channels being associated with more frequent and greater movement downstream). However, sampling of additional reaches and streams with a wider range of gradients and channel types is needed to test the relationship between movement direction and channel type and (or) gradient, and rule out the influence of habitat dewatering. Our results were consistent with the hypothesis that habitat quality rather than social dominance was the primary factor affecting movement by coho salmon in our study streams, and that movers were neither initially inferior to those that remained nor were they less likely to thrive. This is an important perspective on the behavioral ecology of juvenile anadromous salmonids, and also has implications for the design and interpretation of studies on habitat quality, restoration, and salmonid populations as well as the management of those populations. For example, stream road-crossings and smolt counting fences should be designed to accommodate the upstream movements of juvenile anadromous salmonids and movement studies should be designed to detect movements at multiple spatial and temporal scales. Finally, substantial portions of the habitat in the study streams dewatered, which is likely an important factor in the ecology of movement in streams that are regularly or occasionally intermittent. If late summer dewatering occurs regularly, then the propensity to move in the summer would be an advantage. Thus, declining discharge may be both a proximate stimulus and an evolutionary pressure affecting salmonid movement.

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The functional response of drift-feeding Arctic grayling: the effects of prey density, water velocity, and location efficiency

W. John O'Brien, Michael Barfield, and Karen Sigler

Abstract: An important aspect of a predator–prey system is the functional response of the predator to changing prey densities. We studied the feeding rate response of drift-feeding Arctic grayling (*Thymallus arcticus*) on a small invertebrate prey, *Daphnia middendorffiana*, at densities ranging from 0.01 L^{-1} to 1.8 L^{-1} and current velocities of 25, 32, and 40 $cm \cdot s^{-1}$. We videotaped the feeding of grayling to determine the duration of the search and pursuit components of the feeding cycle and the location efficiency of grayling feeding at different current velocities. Feeding rate increased approximately as the prey density to the 0.4 power from 0.01 to 1.25 prey$\cdot L^{-1}$, above which the feeding rate dropped. Current velocity had no significant effect on feeding rate. Search and pursuit times dropped with increasing prey density, but neither was affected by current velocity. However, current velocity reduced both maximum location distance and location efficiency. The lack of increase in feeding rate with increasing current velocity may be due to a trade-off between the increasing likelihood of encounter and decreasing location efficiency as current velocity increases. These data suggest that grayling could effectively feed in a variety of stream habitats with different current velocity.

Résumé : Un aspect important du système prédateur–proie est la réponse fonctionnelle des prédateurs aux changements de densité des proies. Nous avons étudié chez l'Ombre arctique (*Thymallus arcticus*), un poisson qui se nourrit dans la dérive, la variation du taux d'alimentation à même des *Daphnia middendorffiana*, de petites proies invertébrées dont la densité variait de 0,01 L^{-1} à 1,8 L^{-1} à des vitesses de courant de 25, 32 et 40 $cm \cdot s^{-1}$. L'alimentation de l'ombre a été enregistrée sur bande vidéo pour déterminer la durée des composantes de recherche et de poursuite du cycle alimentaire et l'efficatité de la localisation de la proie durant l'alimentation à diverses vitesses de courant. Le taux d'alimentation augmente à peu près en fonction de la densité des proies à un exposant de 0,4 à des densités de proies variant de 0,01 et 1,25 proie$\cdot L^{-1}$; au-delà de ces valeurs, le taux diminue. La vitesse du courant n'affecte pas de façon significative le taux d'alimentation. Le temps consacré à la recherche et à la poursuite diminue en fonction inverse de la densité des proies, mais n'est pas affecté par la vitesse du courant. Cependant, la vitesse du courant diminue la distance maximale de localisation et son efficacité. L'absence d'augmentation du taux d'alimentation en fonction de la vitesse du courant peut être due à un compromis entre la probabilité plus élevée de rencontre à une vitesse de courant élevée et la baisse de l'efficacité de la localisation. Ces observations indiquent que l'ombre peut s'alimenter de façon efficace dans une gamme étendue de cours d'eau à diverses vitesses de courant.

[Traduit par la Rédaction]

Introduction

One of the most important aspects of foraging is the relationship between prey density and feeding rate, commonly referred to as the functional response of the predator. Solomon (1949) was the first to introduce the idea that Holling (1959*a*, 1959*b*, 1965) later explored in detail. The standard way of modeling the functional response is to divide the total time per prey into search time and pursuit (handling) time (Pulliam 1989). Search time is often modeled by assuming a random prey distribution and a random search. If a constant volume is searched per unit search time, then the functional response is given by the disk equation (Holling 1959*b*; Pulliam 1989):

$$FR = \frac{a\rho}{1 + a\rho h}$$

where FR is the feeding rate, a is the attack rate, ρ is the prey density, and h is the handling (including pursuit) time. This is an example of a Type 2 functional response (Holling 1959*a*), which increases at a steadily decreasing rate until reaching a plateau. At low prey densities, FR is proportional to ρ (which is assumed also in many other functional response models), whereas at high prey density, FR approaches a constant value of $1/h$.

Whereas the functional response has been studied in many animal groups, both vertebrate (Witz 1996; Morgan et al. 1997; O'Donoghue et al. 1998) and invertebrate (O'Neil

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1997), there is relatively little known about the functional response of fish, especially drift-feeding fish. The general foraging ecology of fish has been well studied (Lazzaro 1987; O'Brien et al. 1990; O'Brien and Evans 1992) in part because of their ease of handling and relatively straightforward behavior. Drift feeding in streams, in particular, has attracted a lot of interest (Dahl and Greenberg 1998) because of its importance to the growth and well-being of stream fish (Deegan et al. 1997), as well as its potential impact on drifting invertebrates (Friberg et al. 1994). There is not, however, a great deal known about drift feeding in Arctic grayling. O'Brien and Showalter (1993) demonstrated that the search window width (greatest lateral distance at which prey are attacked after excluding the lateral-most 5% of attacked prey on each side) of drift-feeding Arctic grayling (*Thymallus arcticus*) was reduced with increasing current velocity and increased debris in the stream water. The width of the search window declined from about 80 cm at a low velocity (11.6 $cm \cdot s^{-1}$) to 45 cm at the highest velocity tested (55.7 $cm \cdot s^{-1}$) (O'Brien and Showalter 1993). There is preliminary evidence that velocity not only reduces the size of the search window but may also erode the efficiency of location within the window. Interestingly, Hughes (1992*a*, 1992*b*) found that grayling generally preferred the most rapid water that was available in a small mountain stream.

The functional response is "essential in developing models of foraging behavior and ecological interactions"; for example, the form of the functional response can determine the stability of a predator–prey system, the magnitude of fluctuations in prey density, and the nutrition of the predator (Abrams 1990). For drift-feeding Arctic grayling, their prey (stream aquatic insects) often have synchronized hatches and emergences that at these times could produce large numbers of prey in the drift. At other times and locations, the density of prey in the drift may be very low (for example, data in Hinterleitner-Anderson et al. 1992 show a 25-fold range of *Baetis* densities). Therefore, grayling may feed at many different prey densities.

In this work, we directly investigated the effect of increasing prey density and stream velocity on the feeding rate of Arctic grayling and on the average time that the fish spent searching (related to the attack rate in the disk equation) and attacking each prey (the overwhelming majority of handling time). We also attempted to estimate the probability that a prey item at a given water velocity and location lateral to a searching fish was located as it passed (location efficiency). We hypothesized that feeding rate would be proportional to prey density at low densities and then level off at high prey densities. We also hypothesized that feeding rate would increase, and location efficiency would decrease, with increasing current velocity.

Materials and methods

We investigated the drift feeding of Arctic grayling at the Toolik Lake Field Station (TLFS) on the shores of Toolik Lake, Alaska (68°38′00″, 149°36′15″). Two to four fish were observed each summer from 1995 to 1997 (location efficiency estimation was based on similar experiments in 1992). The fish, 31.5–34.5 cm total length, were obtained from a wild population in the Kuparuk River about 8 km north of Toolik Lake. The Kuparuk has only large adult fish, with small fish inhabiting its tributaries (Deegan et al. 1997).

The experiments were done in a 500-L experimental stream designed after Vogel (1981). Water was filtered daily so the turbidity was low. The stream was housed in a 4-m-high "polar tent" with a semitranslucent fabric that allowed about 20% full sunlight. Grayling visual acuity (measured by maximum distance at which they respond to prey) is fairly constant above about 1000 lx (Schmidt and O'Brien 1982). Because light level during the trials was above this, they were not believed to be an important factor. The observation portion of the stream is 1.5 m long and 0.61 m wide (with water depth of 0.16 m) with Plexiglas® windows on each side. Water was recirculated (moved from the back to the front of the channel) through a 25-cm-diameter pipe using a propeller driven by an electric motor. A rheostat regulated the speed of the propeller giving stream velocities up to 65 $cm \cdot s^{-1}$. The front end of the stream is fitted with a diffuser to spread the current across much of the stream width and with flow straighteners to reduce turbulence (see O'Brien and Showalter 1993 for more details).

Feeding rate experiments

A given experiment (run) consisted of feeding a single fish on a constant density of small prey, *Daphnia middendorffiana*, 2.5–3.0 mm long. *Daphnia middendorffiana* were used as prey because they are similar in size to stream-drifting invertebrates, they are nearly uniform in size, and large numbers of them can be easily collected from a nearby pond (pond MS-1, 50 m east of TLFS). The major drift species in the Kuparuk is the mayfly *Baetis*, which varies in length from about 2 to 4 mm (Lee and Hershey 2000). In 1995 and 1996, prey densities used were from 0.01 to 1.25 $prey \cdot L^{-1}$ (a total of 41 runs). Because the feeding rate did not saturate in that range, additional runs were done at high densities (0.6–1.8 $prey \cdot L^{-1}$) in 1997 (24 runs), but only at slow and medium water velocities. In all experiments, the initial prey density was created by slowly adding the appropriate number of prey to the back of the stream behind the fish. The prey were added over a time period calculated to equal the turnover time of the stream at the current velocity being used. The prey density was kept constant by adding a prey item each time the fish ate a prey item. Prey were added at the back of the stream, out of sight of and behind the fish. The experiment was continued until the fish had fed on slightly more than 100 prey. The feeding was videotaped using a Panasonic Palmcorder® PV-IQ204 mounted 1.2 m above the stream. Because prey were not visible on the videotape, an observer (who could see the prey) looking into the side of the stream indicated each attack verbally and kept track of the number of attacks and total time elapsed.

Feeding rates were determined at three different average stream velocities: 25, 32, and 40 $cm \cdot s^{-1}$ (peak velocity about 35, 45, and 55 $cm \cdot s^{-1}$, respectively). Stream velocity was measured with a Marsh-McBirney current meter (Marsh-McBirney, Inc., Frederick, Md.) at 5-cm increments across the channel (see Fig. 1). Water temperature was maintained at 12°C using an Aquanetics® chiller (Aquanetics Systems, San Diego, Calif.), which automatically warms or cools the water. For data presented here, each fish was used at all prey densities for that year (0.01, 0.05, 0.25, and 1.25 L^{-1} for 1995–1996; 0.6, 0.9, and 1.8 L^{-1} for 1997).

It was not possible to completely plan the experiment. Grayling are extremely agonistic and subdominant fish will not feed, so they had to be kept separate. Also, fish had to be held for 4–8 days before they were used for feeding trials. Some fish would not feed in the experimental stream, others would feed for a number of runs and then refuse, and others could be used for many runs. Therefore, the data is based on a fairly small number of fish and predominantly those that tended to be the most willing to feed in the experimental stream.

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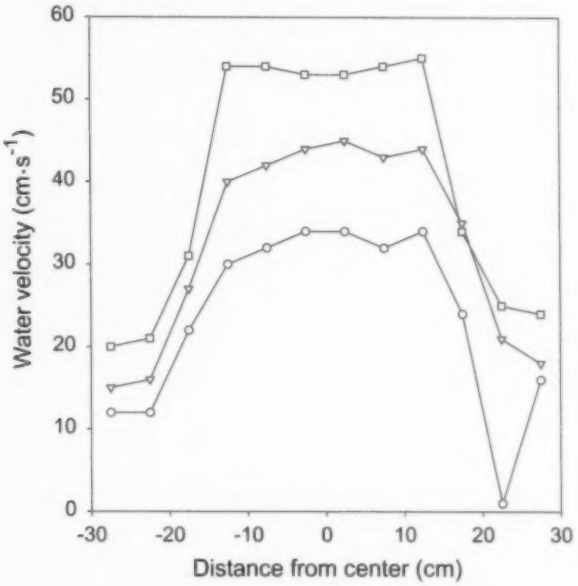
Fig. 1. Current velocity across the experimental stream. The average velocities are 25 cm·s^{-1} (circles), 32 cm·s^{-1} (squares), and 40 cm·s^{-1} (triangles).



Feeding cycle components

The Palmcorder® tapes were analyzed using a Panasonic AG-6300 tape deck with a Panasonic Remote Controller A505. The time and position of the fish at the start and end of each attack was determined, from which search times and pursuit times were determined. Pursuit time is the length of time that it takes the fish to swim to a located prey and attack it. Because the fish apparently immediately searches after an attack, the time from one attack until the start of the next pursuit was considered to be the search time.

Location efficiency experiments

We also analyzed a series of 13 runs using five stream velocities at a prey density of 0.01 L^{-1} performed during 1992 using the procedure described above. We attempted to estimate the location efficiency, which is the probability that a prey item is attacked as it passes a fish searching for prey (we call it location efficiency because we assume that the fish attacks any prey it locates). This location efficiency is assumed to be a function of prey velocity and the lateral distance from the fish to the path of the prey item. Because the prey used cannot be seen on the videotapes, location efficiencies could not be determined by simply dividing the number of prey attacked by the total that pass the fish at a given velocity and position. However, it can be shown that if the prey are randomly distributed, the maximum likelihood estimator of the location efficiency is the number of prey attacked divided by the expected value of the number that pass the fish (at a given velocity and position). Therefore, we assumed that the prey were randomly distributed (because of mixing in the return channel) and traveled at the water velocity in straight lines parallel to the sides of the stream. The prey can swim in still water, but the distance they could travel in the few seconds that it takes to traverse the channel would likely be negligible. Because we measured water velocity in 5-cm increments, we conceptually divided the width of the stream into twelve 5-cm-wide "tracks" across the width of the stream. From the videotapes, we determined the fish location (track) at all times, from which we calculated the expected number of prey passing the fish for each fish track – prey track combination. This was the product of the prey density, water velocity at the prey's location, track cross-sectional area, and time that the fish was in the given track. We also noted the location of the fish when it began to move toward each prey item (presumably its position when it located the prey item) and the position at which it ate the prey item. This allowed us to determine the actual number of attacks for each fish track – prey track combination. Using the water velocity of each prey track, we were able to estimate the efficiency as a function of lateral distance and water (prey) velocity.

These experiments were done at a very low prey density (0.01 L^{-1}, which is five prey in the entire system) to minimize the chance that the fish would be attacking one prey item as another passed. Because five different rheostat settings were used and there were 12 generally different current velocities across the stream for each, there were a large number of velocity – lateral distance pairs (39 velocities and 12 lateral distances). The expected and observed number of prey items for each was generally less than 10, so the ratio would be very inaccurate. Therefore, to give the efficiencies, the data were lumped into ranges of stream velocity and lateral distance, and then the ratio of the total attacked prey to expected number of prey was determined for each; this gives the best estimate as long as efficiency is constant across each range of velocities and distances. A total of 639 prey items were captured in these runs, the expected number of prey ranging from 9.7 to 253 for the different efficiencies calculated (all expected prey numbers were above 50 except at the most lateral distance).

Statistical analysis

The feeding rates and attack and pursuit times were analyzed using regression and analysis of variance (ANOVA). The factors affecting these dependent variables were prey density (the covariate in the regressions), water velocity, the individual fish used, and their interactions. The 1996–1997 data spanned a wide range of prey densities (0.01–1.25 L^{-1}), and each fish was used at each density for at least one of the water velocities. Therefore, these data were first analyzed without the 1997 data. For the regressions, we excluded only terms involving interactions between the fish and water velocity (because we did not have data for each fish at each velocity), allowing us to test for effects of density, velocity, and individual fish and interactions between density and the other two factors. Logarithmic transformations of the dependent variables and prey density gave linear relationships, homogeneous variance, and normal residuals. We then performed the regressions including 1997 data at 0.6 prey·L^{-1} and 0.9 prey·L^{-1}, because these are within the range of densities for 1995–1996. One reason for initially excluding these data is that by their inclusion, the tests of the effect of the individual fish and the fish–density interaction could be influenced by the fact that different densities and a narrow range of densities were used in 1997. Because these terms were not significant using the 1995–1996 data, it should be possible to include the 1997 data (except at the highest density) in the regression of the dependent variables on prey density alone.

For the ANOVAs, because we did not have replicates for each fish at each prey density and water velocity, we excluded any terms involving the individual fish and so tested for the effect of prey density, water velocity, and their interaction. The dependent variables were again logarithmically transformed. ANOVAs used only 1995–1996 data, because one water velocity was absent in the 1997 data.

For the location efficiency data, differences between each pair of water velocities at the same lateral distance were tested. Under the null hypothesis that the efficiencies were the same (equal to the efficiency obtained by combining the data for the two velocities), we calculated the expected number of prey captured for each velocity. Under the assumptions made, the actual number captured

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should be a Poisson random variable with this mean, so this distribution was used to test the significance of the difference.

Results

Feeding rate experiments

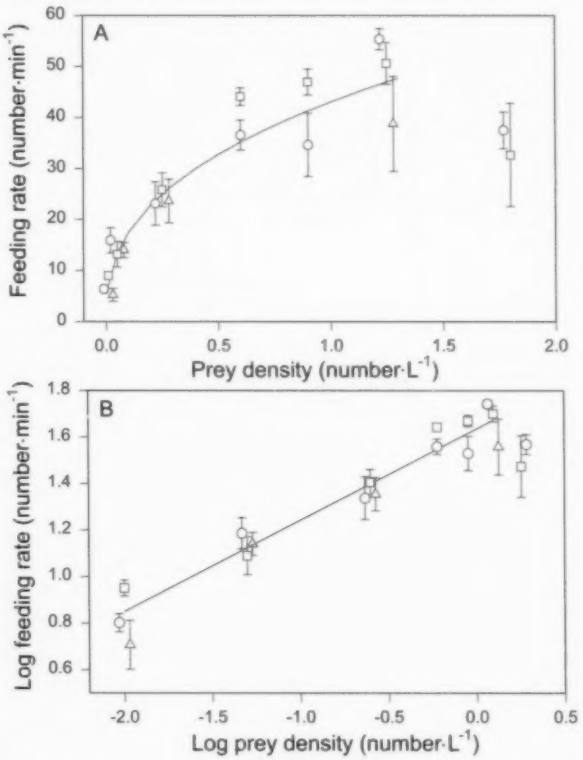
The feeding rates are shown in Fig. 2*a*. The feeding rate increases with prey density up to 1.25 L^{-1} and then falls at 1.8 L^{-1}. There is no apparent consistent effect of stream velocity. We first analyzed the 1995–1996 data, which included prey densities of 0.01, 0.05, 0.25, and 1.25 L^{-1}, using all data for which we had at least one run at each density for each fish. We performed a regression for the logarithm of the feeding rate, with logarithm of the prey density as a covariate and the individual fish and stream velocity and interactions between each of these and prey density as other factors. (We could not test for fish–velocity interactions because we did not have data for each fish at each velocity.) The prey density was highly significant ($p < 0.001$), but all other factors were not ($p > 0.4$ in all cases). We also performed an ANOVA with prey density and speed (and their interaction) as factors. Density was again highly significant ($p < 0.001$), whereas speed ($p = 0.187$) and speed–density interaction ($p = 0.374$) were not. We then performed a regression of logarithm of feeding rate on logarithm of density (eliminating the factors not found to be significant) and obtained the relation $FR = 41.1\rho^{0.381}$. This regression had $R^2 = 0.82$ and a lack-of-fit $p = 0.769$, indicating that the regression fit the data well.

For the 1997 data, prey densities of 0.6 L^{-1} and 0.9 L^{-1} fell within the range of densities for the above regression. The mean feeding rate at 0.9 L^{-1} was almost exactly on the regression line given above, whereas at 0.6 L^{-1}, it was a little higher. However, the prey density of 1.8 L^{-1} fell outside the range of the previous regressions, and the average feeding rate was well below the regression, indicating the relation above does not hold above 1.25 prey·L^{-1}. We therefore repeated the regressions described above for all data except that at 1.8 prey·L^{-1} and again found that the fish, speed, and their interactions with density were not significant ($p > 0.15$), whereas density was highly significant ($p < 0.002$). The regression using only density gave a relation of $FR = 43.0\rho^{0.392}$ with $R^2 = 0.84$ and again a good fit (although in this case the residuals are borderline normal, with $p = 0.056$ on the Anderson–Darling test). A plot of the feeding rate data with logarithmic axes and including the regression line is shown in Fig. 2*b* (the same regression line is also shown in Fig. 2*a*).

Search and pursuit times

The two major components of the feeding cycle of drift-feeding grayling are search and pursuit of located prey. Search time (t_s) is dramatically affected by prey density, falling from an average of 7.9 s at the lowest density measured to under 1.3 s for all densities of 0.6 prey·L^{-1} or greater. Regressions and ANOVAs as described for the feeding rate were performed on the logarithms of search and pursuit times. Regression results presented here include all prey densities except 1.8 L^{-1}, but the results using 1995–1996 data alone were similar. For search time, none of fish, speed, or the interaction of either with density was significant ($p > 0.35$), whereas the logarithm of density was highly significant ($p < 0.001$). Only the density was significant for the ANOVA. The regression equation using only the density was $t_s = 0.863\rho^{-0.476}$ with $R^2 = 0.82$, a goodness-of-fit $p = 0.52$, and a regression $p < 0.001$ (Fig. 3). Therefore, the search time did not drop as the reciprocal of the density (as often assumed, as in the disk equation), but approximately as the reciprocal of the square root of the density. The search time was higher than the regression at a prey density of 1.8 L^{-1}.

Fig. 2. Feeding rate of Arctic grayling as a function of *Daphnia middendorffiana* density for different current velocities. The average water velocities are 25 cm·s^{-1} (circles), 32 cm·s^{-1} (squares), and 40 cm·s^{-1} (triangles). Bars indicate ± standard error, with sample sizes generally 3 or 4 (in two cases each, the sample size is 2 or 5). Some of the points have been offset horizontally a small amount for clarity. (*a*) Linear scales on axes. (*b*) Base-10 logarithmic scales.



With pursuit time (t_a), the speed–density and fish–density interactions were close to significant ($0.05 < p < 0.1$), whereas speed ($p = 0.166$) and fish ($p = 0.775$) were not. Density was again highly significant ($p < 0.001$). For the ANOVA, water velocity was highly significant ($p < 0.001$), and the water velocity–density interaction was almost significant ($p = 0.06$). On average, slower water velocity led to longer pursuit times. The regression equation using only density was $t_a = 0.540\rho^{-0.130}$, which was highly significant ($p < 0.001$) with $R^2 = 0.64$ and a goodness-of-fit $p = 0.68$. Pursuit time, therefore, decreased slowly with increasing density (except at the highest density, see Fig. 3). Because

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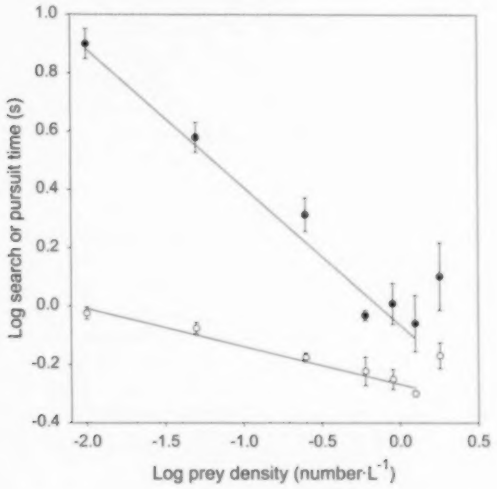
Fig. 3. Search and attack time of Arctic grayling feeding on different densities of *Daphnia middendorffiana* (both axes are logarithmically transformed). Solid circles represent search times, and open circles represent pursuit times. Bars indicate ± standard error, with sample sizes from 6 to 12.



the search time was much higher at most densities, the pursuit times are generally less important.

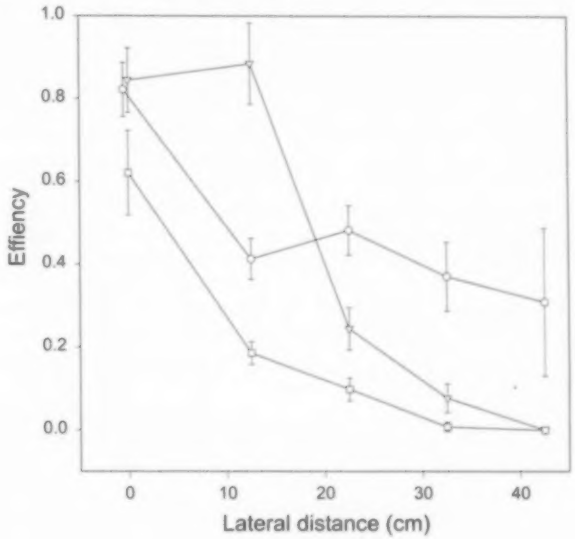
Location efficiency experiments

Increased stream velocity reduced the efficiency with which grayling located prey (Fig. 4). There is some irregularity at 12 cm lateral distance from the fish. At all other distances, the efficiencies decline in order of velocity. There is much uncertainty about each value, because it is determined by dividing by the expected number of prey. The actual number can depart significantly from the expected value owing to chance and to a nonrandom distribution of prey. However, we are mostly interested in the apparent fact that the efficiency averaged across the channel decreases with increasing water velocity. This seems quite likely, and the data in this figure support that hypothesis, at least at the highest velocity. Notice that there is not 100% efficiency, even right in front of the fish. Given our assumption of random prey and a constant efficiency across each range of water velocities and lateral distances, the number of prey caught for each point is a Poisson random variable. This distribution was used to construct the error bars shown and to test for differences owing to water velocity at each lateral distance (a cutoff of $p = 0.05/3$ was used because there were three comparisons each). The three efficiencies at 0 lateral distance did not differ significantly, nor did the medium and fast water results at the two most lateral positions. All other differences were significant under the assumptions given (which may understate the error of each estimate).

Discussion

Drift-feeding Arctic grayling show a functional response that is a Type 2 functional response, except for the decrease at the highest density. The feeding rate at the lowest prey density (0.01 L^{-1}) is about 5–8 prey·min^{-1}. The feeding rate

Fig. 4. Location efficiency of Arctic grayling feeding on low densities of *Daphnia middendorffiana* at different water velocities. Velocites range from 6 to 25 cm·s^{-1} (circles), 26 to 45 cm·s^{-1} (triangles), and 46 to 65 cm·s^{-1} (squares). Bars indicate ± standard error. The low-velocity point at 0 lateral distance has been offset slightly for clarity.



rises at prey densities up to 1.25 prey·L^{-1} and then drops at the highest prey density. The feeding rate is usually expected to approach a plateau at high densities (for example, all of Holling's types), and that is what we expected to find when we ran the 1997 high-density runs. The feeding rates at 0.6 prey·L^{-1} and 0.9 prey·L^{-1} were similar, and that at 1.25 prey·L^{-1} is not a great deal higher, so it is possible that a plateau is reached there. However, a steadily increasing curve (as described by the regressions above) seems to fit the data better. At the highest density, the feeding rate drops. Although it is generally assumed (and often found) that feeding rate plateaus at high density, it is clearly possible that the observed drop in feeding rate at very high density is real. For example, when too many prey are visible at once, the fish may hesitate before attacking; this is consistent with the increase in average search time observed at the highest density.

The feeding rate increase was less than proportional to density even at the lowest densities. A possible reason is that our lowest densities were out of the linear range. Therefore, we plotted the reciprocal of the feeding rate versus the reciprocal of the prey density and the ratio of feeding rate to prey density versus feeding rate (Holling 1959*b*), both of which are linear for the disk equation of Holling (1959*b*). Both plots were curved, indicating that the disk equation does not fit the data.

For all but the highest density, the feeding rate is proportional to about the 0.4 power of the density, so that grayling double their feeding rate with an increase of about five times in prey density. A proportional rate of increase is expected if the fish spends most of its time searching and if the average search time is inversely proportional to the density. The

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measured search times and pursuit times show that most time is spent in search at low prey densities, but the average search time was not inversely proportional to density. Abrams (1990) shows that departures from proportionality may result from the predator either decreasing the proportion of the time it spends in feeding or increasing its attack threshold as prey density increases. Both these (with certain assumptions) lead to an initial increase in feeding rate as the square root of prey density, not far from our results. There is experimental evidence for a drop in predator effort with increasing prey density. For example, Holling (1966) observed that the maximum distance at which a mantis will react to prey increases with increasing hunger. Similarly, grayling may be willing to attack prey further laterally when prey density is low and concentrate on closer prey at high density. This would certainly make sense in maximizing net energy gain. The average lateral distance of attacked prey does decrease with increasing density but not enough to totally account for the slow increase in functional response. However, it may be that the grayling has a higher attack threshold at higher prey density, which only incidentally affects lateral distance of attacks.

Another interesting aspect of the functional response is the lack of effect of stream velocity. Although increased velocity should cause the fish to encounter more prey, the feeding rate did not significantly change. This cannot be accounted for solely by the reduction in the search window with increasing water velocity that O'Brien and Showalter (1993) reported. They reported a 33% decrease in window width with stream velocity increasing from below 20 $cm \cdot s^{-1}$ to almost 60 $cm \cdot s^{-1}$. Further, they predicted that feeding rate would increase with increasing velocity, at least for velocities from 10 $cm \cdot s^{-1}$ to 45 $cm \cdot s^{-1}$. Clearly this is incorrect.

One possible explanation for feeding rates not increasing with increasing stream velocity is that the search window width and location efficiency decrease as a function of stream velocity. This could have the effect of keeping grayling feeding rates about constant with changing stream velocities. For the lowest density, multiplying the stream velocity, cross-sectional area, prey density, and average efficiency gives an estimate of the expected feeding rate. These values are 7.7, 9.5, and 6.1 $prey \cdot min^{-1}$ for low, medium, and high water velocities, respectively, compared with observed feeding rates of 6.4, 9, and 5.2 $prey \cdot min^{-1}$. At higher prey densities, the effect of stream velocity should be reduced because the grayling spends less time searching and more in pursuit. Even without the drop in efficiency, because the highest stream velocity used was only 60% higher than the lowest and the feeding rate increased only as the 0.4 power of prey density, the effect of stream velocity should not be great (about 20%, because $1.6^{0.4} \approx 1.2$).

Given that the feeding rate does not increase with current velocity, one might expect that grayling in a natural stream would select feeding positions in slow currents where respiratory costs should be lower. Hughes and Dill (1990) found that removing swimming costs from their model made little or no difference to the predictions as to what current velocity the fish might choose. Furthermore, they found that grayling commonly chose feeding positions in water as rapid as 55 $cm \cdot s^{-1}$, although they also chose slower current positions. We also observed grayling feeding in currents as high as 55 $cm \cdot s^{-1}$ in the Kuparuk River, and in an experimental stream where two different flow velocities could be created, grayling consistently chose to be in the faster current (O'Brien, personal observation). Hughes (1992*a*, 1992*b*) also found that dominant Arctic grayling chose the most rapid current available, whereas subdominant (i.e., smaller fish) settled for feeding sites in slower water. Interestingly, there are no "small" grayling in the Kuparuk River, suggesting that big fish take most, if not all, profitable feeding sites and smaller, subdominant fish cannot grow (Deegan et al. 1997). Consistent with this idea that most if not all profitable feeding sites are taken is the fact that many fish lose weight during years of low flow where there may be fewer profitable feeding sites (Deegan et al. 1999).

Although grayling are adept swimmers and do not have to swim very hard at these high stream velocities, they still expend more energy at high velocities than at low velocities. One possible advantage to being in fast flowing water is that attack distances are very short owing to reduced search window width. This would mean less time and energy spent attacking each prey, possibly resulting in an energy savings and an increase in the percentage of time spent searching. Also, faster currents may be able to carry larger prey.

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Cellular and tissular distribution of copper in an intrasedimentary bivalve, the Baltic clam *Macoma balthica*, originating from a clean or a metal-rich site

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Abstract: Baltic clams (*Macoma balthica*) from clean and industrialized areas were exposed to 30 ng Cu·mL^{-1} or 40 ng Cu·mL^{-1} for 13 days. Specimens from the industrialized site accumulated less Cu in their soft tissues, suggesting that those clams living in a metal-rich area are able to limit metal accumulation. Cu and metallothionein-like protein (MTLP) levels were positively correlated in specimens from the industrialized site only, indicating that perhaps living in a polluted area enables them to use this method of detoxification. The contaminated specimens contained Cu-rich microgranules in the basal lamina and intracellular spaces of digestive gland, labial palps, and gills as well as in lysosomes of the digestive gland and in a few hemocytes. The coexistence of S and Cu suggests that sulfur may be the chelating agent. As a consequence of detoxified storage, ultrastructural damage was rarely observed. These Cu deposits, which contributed to the predominance of biochemical insoluble forms shown in the whole soft tissues, are generally considered hardly available to predators, whereas soluble Cu (35–38% of total Cu) would most probably be bioavailable.

Résumé : Des bivalves *Macoma balthica* provenant de sites propre ou industrialisé ont été exposés à 30 ng Cu·mL^{-1} ou 40 ng Cu·mL^{-1} pendant 13 jours. Les spécimens du site industrialisé accumulent moins de cuivre dans leurs tissus mous ce qui suggère que, vivant dans un site enrichi en métaux, ils peuvent limiter l'accumulation. Les taux de cuivre et de MTLP sont corrélés positivement uniquement chez les animaux du site industrialisé qui seraient donc plus à même d'utiliser ce mode de détoxication. Les spécimens contaminés contiennent des granules riches en cuivre dans la lame basale et les espaces intercellulaires de la glande digestive, des palpes labiaux et des branchies, dans les lysosomes de la glande digestive et dans quelques hémocytes. La coexistence de soufre et de cuivre suggère que le soufre serait l'agent chélatant. Les dommages ultrastructuraux sont rares, en relation avec le stockage du cuivre sous des formes détoxifiées. Les dépôts de cuivre, contribuant à la prédominance de la fraction insoluble dans les tissus mous, sont généralement considérés comme peu assimilables par les prédateurs, contrairement au cuivre soluble (35 à 38% du cuivre total).

Introduction

The Baltic clam *Macoma balthica* is a widespread species in the estuarine and coastal areas of Northwest Europe, representing a consistent fraction of the marine biomass and entering the food web of benthic fish. *Macoma balthica* is also present in North America and the existence of distinct races or even different species depending on the continents is questionable (Beukema and Meehan 1985; Meehan 1985). This possibility has been evoked to explain differences observed in metal metabolism involving metallothionein (MT) in Baltic clams originating from either South England or the American Pacific (Bray et al. 1983; Johansson et al. 1986; Langston and Zhou 1987). Metallothionein is a cystein-rich, heat-stable, low molecular weight protein that binds metals such as Ag, Cd, Cu, Hg, and Zn and thus contributes to metal detoxification. The synthesis of MT is often induced when organisms are exposed to environments contaminated by heavy metals (Amiard and Cosson 1997). In *M. balthica*, detoxification involving the MT system was not recognized in individuals originating from South England and exposed to cadmium (Langston and Zhou 1987). However, the possible role of a MT-like protein (MTLP) binding Ag and Cu has been mentioned in Pacific American specimens of *M. balthica* (Bray et al. 1983; Johansson et al. 1986). In *M. balthica* originating from the estuary of the Western Scheldt, exposure to Cd, Cu, and Zn induced the increase of cytosolic concentrations of metals and metal-binding proteins displaying several of the main characteristics of MTs (Bordin et al. 1994, 1997). In individuals from the Loire Estuary (France), Rigaa et al. (1998) have shown the presence of a Cd-inducible protein exhibiting some characteristics of MTs. In *M. balthica* collected from several Arctic estuaries, cytosolic heat-stable compounds were evidenced by using

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the polarographic assay, suggesting the presence of MT, the concentration of which varied among stations according to Cu contamination in sediments and soft tissues of bivalves (Amiard-Triquet et al. 1998).

Because of the high potential toxicity of Cu and its high concentrations in some estuaries, the response of *M. balthica* to this metal has given rise to numerous studies (Hummel et al. 1997 and literature cited by these authors). However, the physicochemical forms of storage of Cu have not been studied comprehensively, although they govern both the toxicity to the bivalve and the transfer to its predators (Amiard-Triquet et al. 1993). A previous study of the relationship between Cu and condition in *M. balthica* and the relationship with Cu in sediment has shown that Cu concentration was slowly regulated (several weeks), suggesting a fossilization of Cu in mineral granules (Hummel et al. 1997). Other studies suggest a relationship between Cu and MT in *M. balthica* (Bordin et al. 1994, 1997; Amiard-Triquet et al. 1998). Thus, in the present study, the cellular and tissular distribution of Cu was examined in Baltic clams originating from both clean and industrialized areas, considering that the latter could have evolved strategies to prevent metal toxicity (Mason and Jenkins 1995) under the pressure of chronic contamination. According to the data of the French Mussel Watch (RNO 1995), concentrations of Hg, Cd, Cu, Pb, and Zn in mussels originating from the industrialized Loire Estuary are higher than those from the Bay of Somme, which is a nature reserve (Parc du Marquenterre).

Materials and methods

Biological specimens

Macoma balthica were collected in January 1996 from two estuaries (Loire and Somme). They were selected according to their size and the homogeneity was verified a posteriori using the soft tissue weight. No significant differences were shown between means: 0.343 (confidence interval at 99% level, 0.031) and 0.431 g wet weight (confidence interval at 99% level, 0.099) for specimens from the Bay of Somme and the Loire Estuary, respectively. In the laboratory, specimens were acclimated in seawater (salinity 32‰) at 12°C for 1 week before the experiments. Groups of 20 individuals were held in aquaria containing 2 L of filtered (1 µm) seawater (salinity 32‰) and were exposed to Cu at 30 ng·mL^{-1} or 40 ng·mL^{-1} or kept free of contaminant (controls). For all three conditions, experiments were duplicated. Water in each tank was not aerated and was changed every other day. Over the 13 days of exposure, no mortality was observed. At the end of each experiment, specimens devoted to metal and MTLP determinations were frozen at –80°C until analysis, whereas five controls and five specimens exposed to Cu (for each geographical site) were prepared for cytopathological studies and microanalysis.

Compartmentalization

Soft tissues of individual clams were homogeneized in a solution of 20 mM TRIS, 10^{-5} mM β-mercaptoethanol, and 150 mM NaCl adjusted to pH 8.6 (4 mL·g soft tissue^{-1}). The soluble (S1) and insoluble (P1) fractions were separated by centrifugation (25 000 × *g* for 55 min). The soluble heat-stable compounds including MTLP were isolated by centrifugation of the soluble fraction (12 000 × *g* for 10 min) after heat treatment (75°C for 10 min).

MTLP analysis

In the heat-denatured cytosol (S2), the amount of MTLP was determined by differential pulse polarographic analysis (DPP), a technique based on –SH compound determination according to the Brdicka reaction (Brdicka 1933) as described by Thompson and Cosson (1984). A PAR Model 174 Analyzer, a PAR/EG&G Model 303 Static Mercury Drop Electrode (SMDE), and an X–Y recorder (RE 0089) (EG & G Instruments Corporation, Princeton Applied Research, Princeton, N.J.) were used. The temperature of the cell was maintained at 5°C. The standard addition method was used for calibration with rabbit liver MT (Sigma Chemical Co., St. Louis, Mo.) in the absence of purified bivalve MT.

This analytical procedure is based on several characteristics of MTs but does not allow the assertion that the studied molecule is a true MT because purification and sequencing have not been carried out. Thus, later the terminology of MTLP will be preferred.

Analysis of soluble and insoluble copper

The determination of trace elements was performed with extreme caution to avoid secondary contamination from the laboratory, analytical materials, and reagents. The insoluble (P1) and soluble (S1) fractions were heated (65°C; 12 h) with suprapure nitric acid. After digestion, Cu levels in these acid solutions were determined after dilution with deionized water by flame (contaminated clams) or electrothermal (controls) atomic absorption spectrophotometry using the Zeeman effect, described previously by Amiard et al. (1987). A Hitachi Z 8200 spectrophotometer was used in this study. Standard addition analyses were performed in an iso-medium. The analytical methods were validated by intercalibrations organized by IAEA (Coquery and Horvat 1996; Campbell et al. 2000). Total metal concentrations in the whole soft tissues were recalculated from quantities of trace elements in soluble and insoluble fractions determined previously.

Microscopy and microanalysis

This part of the study was carried out on five individual clams exposed to 40 ng Cu·mL^{-1}. Three organs were chosen: the digestive gland, the gills, and the labial palps. Tissues were fixed in 3% glutaraldehyde buffered with 0.2 M Na cacodylate at pH 7.4. Fixative osmolarity was adjusted to 1050 mosmol/kg with 0.35 M saccharose.

For the ultrastructural study, samples were postfixed in 1% osmium tetroxyde in water and, after dehydratation, embedded into Epon–Araldite. Thin sections (50–80 nm) were collected on Cu grids, stained with uranyl acetate and lead citrate, and observed on a Phillips 201 TEM.

For electron probe microanalysis (EPMA), samples were fixed in 3% glutaraldehyde but non-osmicated, thin sectioned (80–100 nm), collected on titanum–carbon-coated grids, and unstained. EPMA was performed on a JEOL JEM 100 CX II TEM. Energy dispersive spectroscopy was done on a Oxford Instruments Model AN 10 000 at 60 kV in 300 or 600 s countings with a 200 µm condensor diaphragm. In these conditions, a very ponctual in situ analysis (20 nm) was possible, only qualitatively.

Statistical analysis

Intergroup differences were evaluated by analysis of variance (ANOVA) and post hoc comparisons were assessed by Scheffé's multiple range test. These tests as well as calculations leading to regression equations were carried out using a standard statistical package (StatView SE + Graphics™, SAS Institute, Cary, N.C.).

Results

Gross concentrations of metals in *Macoma balthica*

Total metal concentrations in the whole soft tissues recalculated from quantities of trace elements in soluble and insoluble fractions are shown in Fig. 1 for both sites. Controls from the clean site (Somme) showed Cu concentrations

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Fig. 4. (*a*) Electron probe microanalysis (EPMA) in the digestive gland of *Macoma balthica*: control from the Bay of Somme. Occurrence of P, S, Ca, and Zn in one of the contiguous granules present in the interstitial space. Some elements such as Fe, Cu, Zn, or Ti appear twice on the spectrum because of the Ka and La X-ray emissions. The most intense peaks at the left of the spectrum are carbon

Fig. 1. Cu concentrations (mean + SD) in the whole soft tissues of *Macoma balthica* originating from clean (Somme) and industrialized (Loire) sites and experimentally exposed to 30 ng Cu·mL^{-1} (hatched bars) or 40 ng Cu·mL^{-1} (solid bars) or kept free of contaminant (open bars).

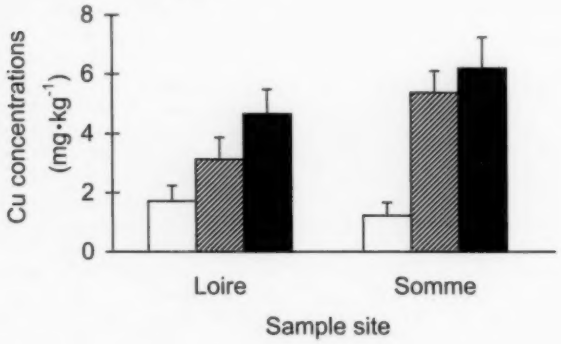
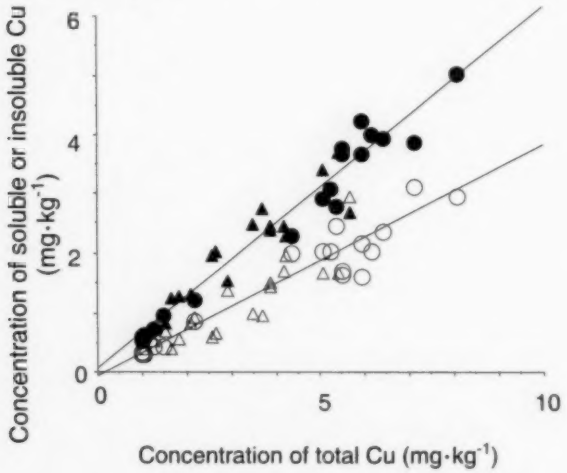


Fig. 2. Relationship between concentrations of soluble (△, Loire; ○, Somme) or insoluble (▲, Loire; ●, Somme) Cu and total Cu (soluble + insoluble) incorporated in the whole soft tissues (mg·kg wet weight^{-1}).



lower than those determined in specimens from the industrialized Loire Estuary (p = 0.08). After exposure, an inverse tendency was observed: the specimens originating from the Bay of Somme had accumulated significantly more Cu than individuals from the Loire Estuary (p = 0.0004 at 30 ng Cu·mL^{-1}, p = 0.01 at 40 ng Cu·mL^{-1}).

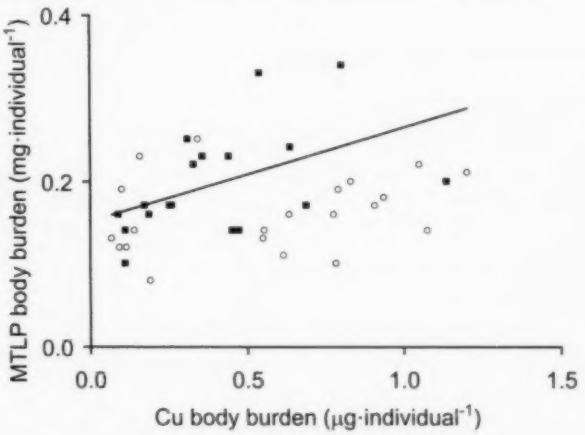
The same pattern was observed when soluble or insoluble Cu levels were taken into account separately and the similarity between the changes in these fractions is clearly reflected through the stability of the percentage of soluble Cu in the whole soft tissues (Table 1). Newly accumulated Cu is distributed among fractions in the same ratios as those existing in the field in either clean or contaminated sites.

Table 1. Relative importance of soluble copper in the soft tissues of Baltic clams originating from the Loire Estuary or the Bay of Somme, experimentally exposed to Cu for 13 days or kept free of contaminants (controls).

	Soluble Cu (% of total Cu)	
	Mean	SD
Loire Estuary		
Controls	36	7
Cu 30 ng·mL^{-1}	35	9
Cu 40 ng·mL^{-1}	37	10
Bay of Somme		
Controls	37	4
Cu 30 ng·mL^{-1}	37	6
Cu 40 ng·mL^{-1}	38	6

Note: SD = standard deviation.

Fig. 3. Relationship between quantities of soluble Cu and metallothionein-like protein (MTLP) (mg·individual^{-1}) in the soft tissues of *Macoma balthica* originating from clean (○, Somme) or industrialized (■, Loire) sites and experimentally exposed to Cu.



Cu distribution between soluble and insoluble fractions in relation to total concentrations of this metal is depicted in Fig. 2. The following equations have been calculated for soluble (Y_1, eq. 1) and insoluble (Y_2, eq. 2) Cu levels. X being the global level of Cu in the soft tissues:

(1) $Y_1 = 0.39X - 0.0714$ with $r = 0.938$, $n = 39$, and $p = 0.0001$

(2) $Y_2 = 0.61X + 0.0714$ with $r = 0.973$, $n = 39$, and $p = 0.0001$

It clearly appears that Cu was stored preferentially in the insoluble part of soft tissues.

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and oxygen originating from the organic matrix. Ti is emitted by the grid, Cl by the resin (Epon). (*b*) EPMA in the digestive gland of *M. balthica* from the Bay of Somme exposed to Cu. Occurrence of P, S, Cu, and Zn in the fine granular material of a lysosome. The granules are ferrous-I. (*c*) EPMA of labial palps of *M. balthica* from the Bay of Somme exposed to Cu. Occurrence of P, S, Ca, Fe, Cu, and Zn. Granules are ferrous-I. Scales bars in µm.

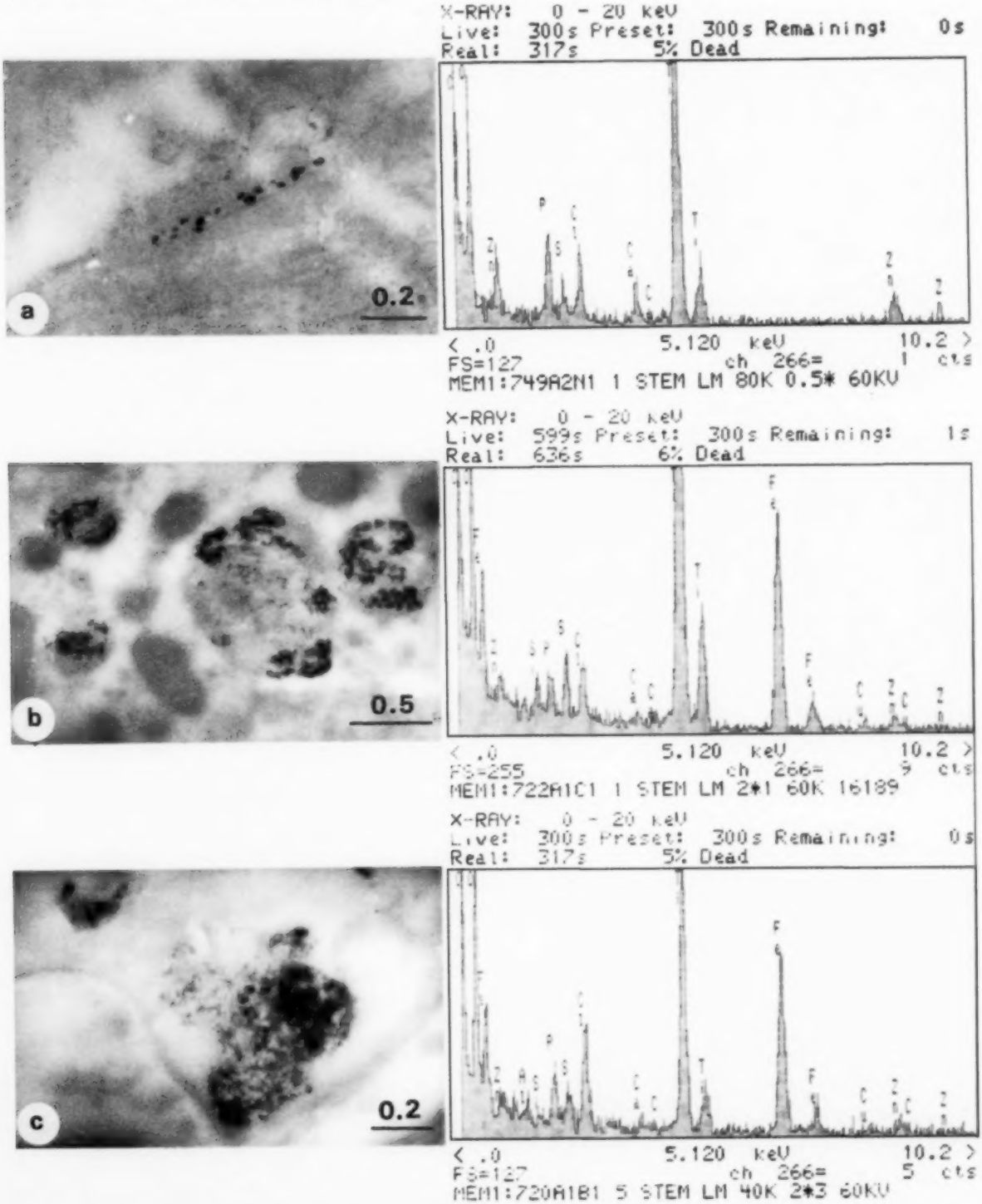

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Fig. 5. (*a*) Electron probe microanalysis (EPMA) in labial palps of *Macoma balthica* from the Loire Estuary exposed to Cu. Occurrence of Mg, Al, Si, S, K, Fe, and Cu in a needle of a lysosome. Notice that Cu is present among the clay particles. (*b*) EPMA in the digestive gland of *M. balthica* from the Bay of Somme exposed to Cu. Occurrence of P, S, Ca, Fe, Cu, and Zn in a granule of the basal lamina. (*c*) EPMA in the digestive gland of *M. balthica* from the Loire Estuary exposed to Cu. Occurrence of P, S, Ca, Cu, and Zn in one of the contiguous microgranules present in the interstitial space between two cells. Scales bars in µm.

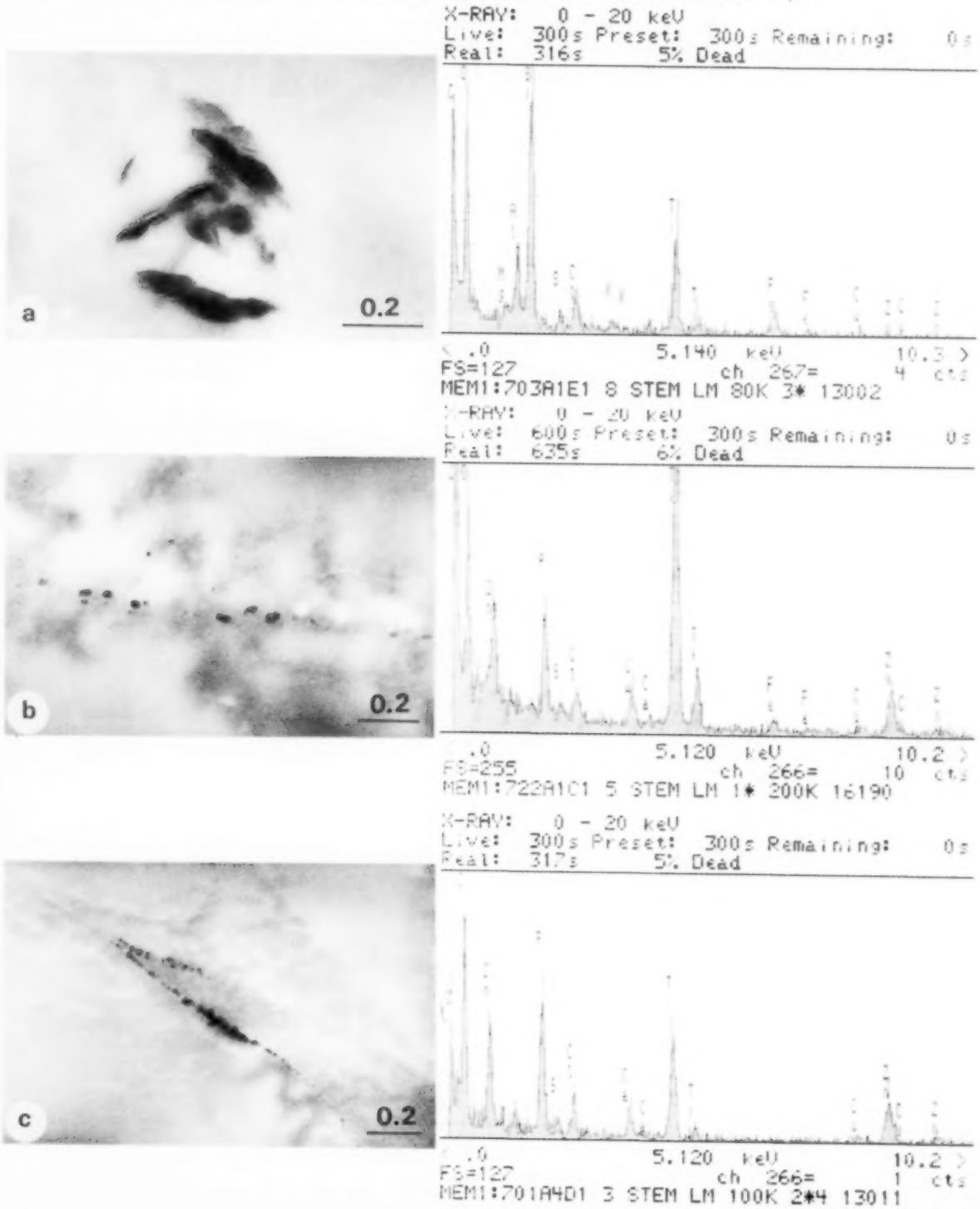

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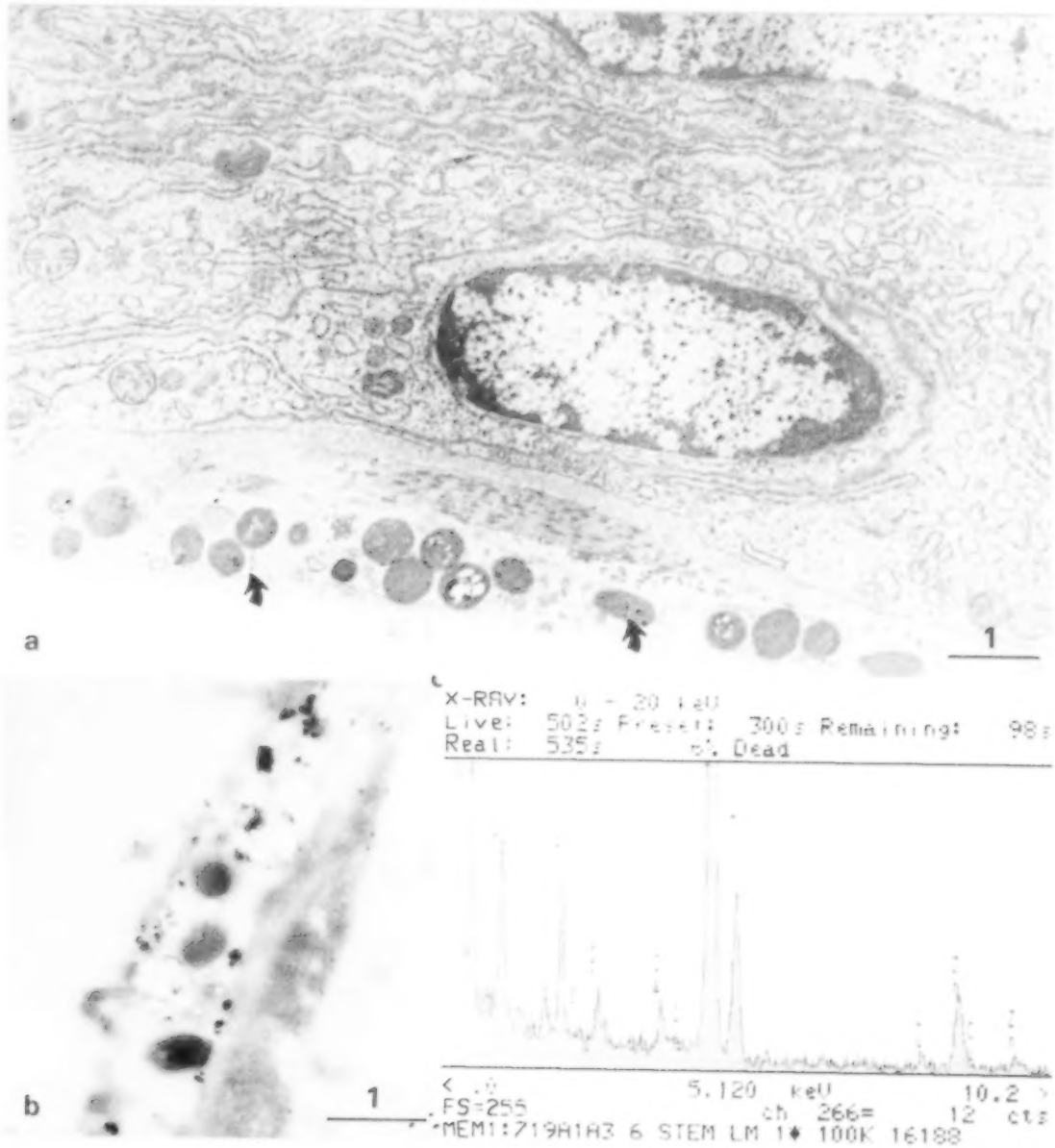
Fig. 6. (*a*) Ultrastructural aspect of digestive gland basal area of *Macoma balthica* from the Bay of Somme exposed to Cu. A granular acidophilic hemocyte containing electron-dense inclusions and cytoplasmic microgranules (arrows) lies under the basal lamina. (*b*) Electron probe microanalysis (EPMA) in the digestive gland of *M. balthica* from the Bay of Somme exposed to Cu. Occurrence of P, S, Ca, Cu, and Zn in microgranules present in the hemocytes. Scales bars in µm.



MTLP concentrations in *Macoma balthica*

It has been shown previously that the weight of individuals has a strong influence on MTLP levels in Arctic populations of *M. balthica* (Amiard-Triquet et al. 1998) but not so marked in populations from the Loire Estuary and the Bay of Somme (Mouneyrac et al. 2000). On the other hand, the influence of weight on Cu concentrations in bivalves has been often mentioned in the literature (Hummel et al. 1997 and literature cited therein) but we have verified that no significant relationships were observed between either soluble or total Cu concentrations and weight in the Baltic clams used in the present study ($p > 0.05$). However, any effect of this factor has been avoided by examining the relationship between Cu and MTLP in the whole soft tissues (Fig. 3). To limit the importance of outliers, two specimens of the Loire Estuary showing the highest weights were eliminated and Spearman correlation coefficients were calculated. Because MTLP is a cytosolic heat-stable protein, it would be logical to consider the relationship between MTLP concentrations in the soft tissues and metal concentrations in the supernatant

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Fig. 5. (*a*) Electron probe microanalysis (EPMA) in labial palps of *Macoma balthica* from the Loire Estuary exposed to Cu. Occurrence of Mg, Al, Si, S, K, Fe, and Cu in a needle of a lysosome. Notice that Cu is present among the clay particles. (*b*) EPMA in the digestive gland of *M. balthica* from the Bay of Somme exposed to Cu. Occurrence of P, S, Ca, Fe, Cu, and Zn in a granule of the basal lamina. (*c*) EPMA in the digestive gland of *M. balthica* from the Loire Estuary exposed to Cu. Occurrence of P, S, Ca, Cu, and Zn in one of the contiguous microgranules present in the interstitial space between two cells. Scales bars in µm.

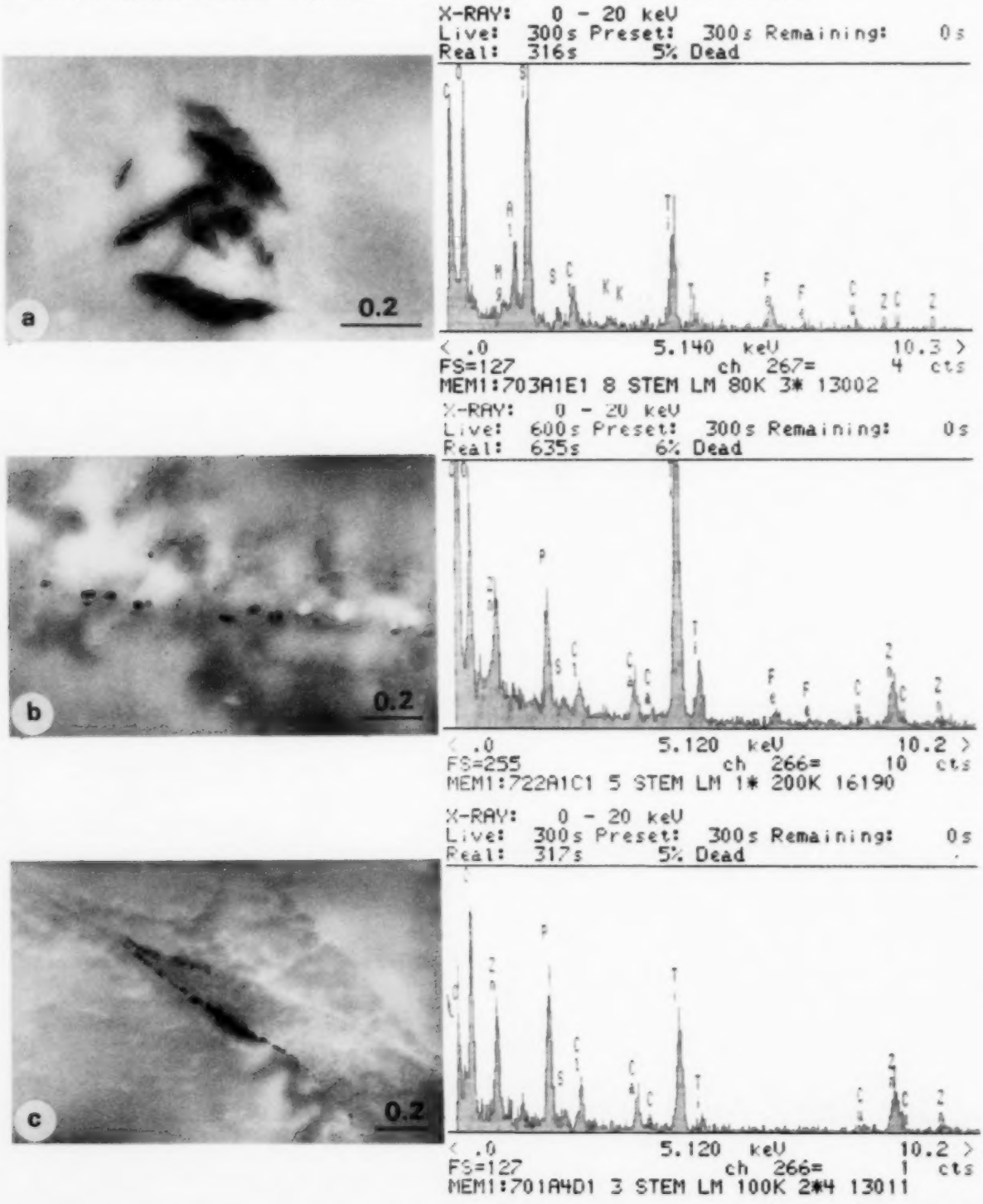

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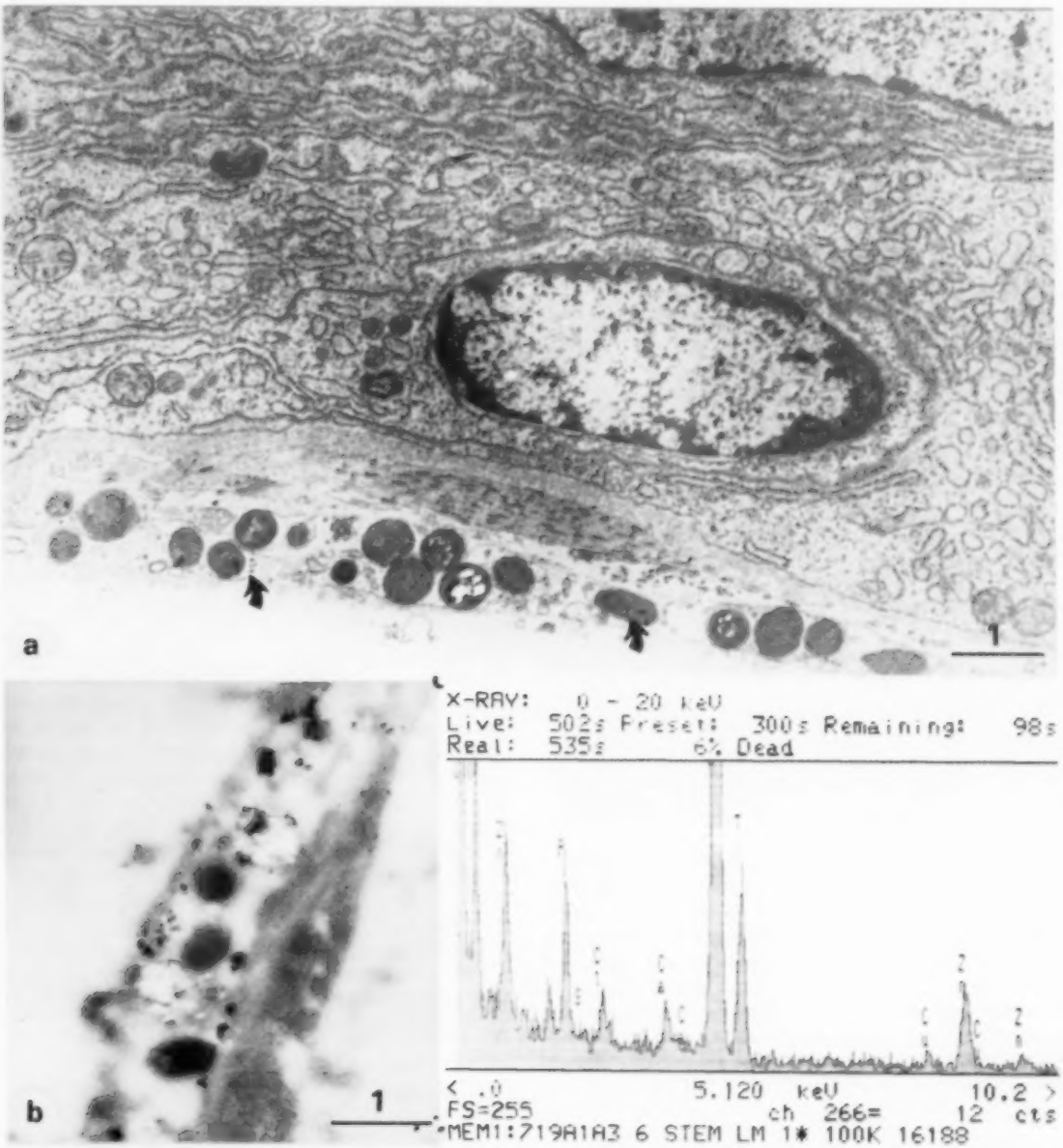
Fig. 6. (*a*) Ultrastructural aspect of digestive gland basal area of *Macoma balthica* from the Bay of Somme exposed to Cu. A granular acidophilic hemocyte containing electron-dense inclusions and cytoplasmic microgranules (arrows) lies under the basal lamina. (*b*) Electron probe microanalysis (EPMA) in the digestive gland of *M. balthica* from the Bay of Somme exposed to Cu. Occurrence of P, S, Ca, Cu, and Zn in microgranules present in the hemocytes. Scales bars in µm.



MTLP concentrations in *Macoma balthica*

It has been shown previously that the weight of individuals has a strong influence on MTLP levels in Arctic populations of *M. balthica* (Amiard-Triquet et al. 1998) but not so marked in populations from the Loire Estuary and the Bay of Somme (Mouneyrac et al. 2000). On the other hand, the influence of weight on Cu concentrations in bivalves has been often mentioned in the literature (Hummel et al. 1997 and literature cited therein) but we have verified that no significant relationships were observed between either soluble or total Cu concentrations and weight in the Baltic clams used in the present study ($p > 0.05$). However, any effect of this factor has been avoided by examining the relationship between Cu and MTLP in the whole soft tissues (Fig. 3). To limit the importance of outliers, two specimens of the Loire Estuary showing the highest weights were eliminated and Spearman correlation coefficients were calculated. Because MTLP is a cytosolic heat-stable protein, it would be logical to consider the relationship between MTLP concentrations in the soft tissues and metal concentrations in the supernatant

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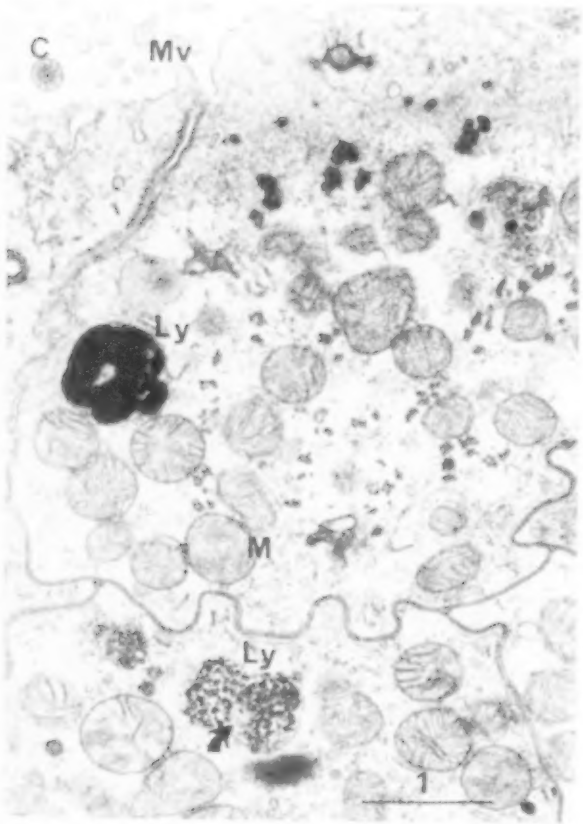
Fig. 7. Digestive cell of *Macoma balthica* from the Bay of Somme exposed to Cu. No cytopathological diseases occur. Note the granular aspect of a lysosome (arrow) probably Fe-rich. C, cilia; Ly, lysosome; M, mitochondria; Mv, microvilli. Scales bars in µm.



obtained after heat denaturation of the cytosol. However, during heating, the distribution of metals among cytosolic compounds may be modified; metal analysis in fractions separated from either total or heat-denaturated cytosol by gel chromatography has shown differences in an other bivalve, the oyster *Crassostrea gigas* (B. Berthet, Service d'Ecotoxicologie, Nantes, France, personal communication). For specimens from the Bay of Somme, increasing Cu did not induce any consistent increase in MTLP. On the contrary, a significant relationship was observed between these factors in specimens from the Loire Estuary:

$$(3)\quad Y = 0.113X + 0.152 \text{ with } r = 0.48,\ n = 18,$$

$$\text{and } p = 0.0248$$

Microanalysis and electron microscopy

In controls from the clean (Somme) and the industrialized (Loire) sites, cells of digestive gland, gills, and labial palps showed absorption features. In the three organs that were able to endocyte particles in suspension in the water or in the digestive tract, epithelium lysosomes contained flakes or needles of Al, Si, K, and Fe. In animals originating from the Bay of Somme only, there was another kind of lysosomes, rich in small Fe particles sometimes associated with P, S, Ca, and Zn. In the basal lamina and intercellular spaces of epithelial cells of the three organs, very small microgranules (15–30 nm) were stored alone or in small groups. These microgranules contained P and Zn with Ca occasionally. Few of these microgranules were observed in clams from both sites (Fig. 4*a*). Cu was not detectable anywhere in the cells. On the other hand, when exposed to Cu, insoluble Cu was detected in all three organs of clams from both sites.

In specimens from the Bay of Somme, clay lysosomes did not store Cu or contained only traces of this element (not shown), but lysosomes including Fe-rich granules stored Cu at detectable levels (Figs. 4*b*, 4*c*). On the other hand, in specimens from the Loire estuary, clay lysosomes contained Cu at detectable levels (Fig. 5*a*). In the three organs of both of specimens, the microgranules of the basal lamina and intercellular spaces were more conspicuous than in controls, at least in specimens from the Loire Estuary. They consisted of P, S, and Zn or sometimes P, S, Ca, Fe, and Zn and frequently contained Cu (Figs. 5*b*, 5*c*). The microgranules could be aligned (Fig. 5*b*) on large zones but the process was too discrete to emphasize a difference between the specimens from one site or the other.

Near the digestive gland, hemocytes of the granular acidophilic type, similar to those described by Auffret (1989) in *Crassostrea gigas*, appeared under the basal lamina of the epithelium (Fig. 6*a*). In these cells, some microgranules were present in both electron-dense inclusions and cytoplasm (Fig. 6*b*). Storage of P, S, Ca, Cu, and Zn in microgranules is depicted in the spectrum shown in Fig. 6.

Ultrastructural damage was rarely observed in the three studied organs from clams exposed to Cu. In specimens from the two sites, all digestive gland cells exhibited organelles similar to those of controls (specimen from the Bay of Somme is shown in Fig. 7). On the other hand, in some areas of the gills and labial palp epithelium, cytological diseases were sometimes noticed, mitochondria being partially deprived of cristae (e.g., labial palps in clams from the Bay of Somme, Figs. 8*a*, 8*b*). The rough endoplasmic reticulum cisternae and the nuclear envelope were swollen (Figs. 9*a*, 9*b*). Generally, in these two organs, at the apical membrane level, microvilli and cilia were similar to those of controls and the membrane was never disrupted (Fig. 9*b*). In these cells, many lysosomes contained needles or granules (Figs. 8*a*, 9*a*) probably corresponding respectively to clay minerals or Fe-rich lysosomes described above (Figs. 4*b*, 4*c*, 5*a*).

Discussion

The concentrations of Cu determined in *Macoma balthica* from the Somme and Loire estuaries agree with the data of the French Mussel Watch (RNO 1995), indicating that the Bay of Somme is relatively clean compared with the industrialized Loire Estuary. However, the intersite difference was not so marked in *M. balthica* than in mussels, which agrees with the finding that Balthic clams are not among the Molluscan species characterized by a strong mineral bioaccumulation at the ultrastructural level. The oyster *C. gigas* exposed to 20 ng·mL^{-1} of Ag for 14 days stored numerous needles of Ag which invaded the whole basal lamina of the digestive gland and the gills, and the lysosomes also stored abundant

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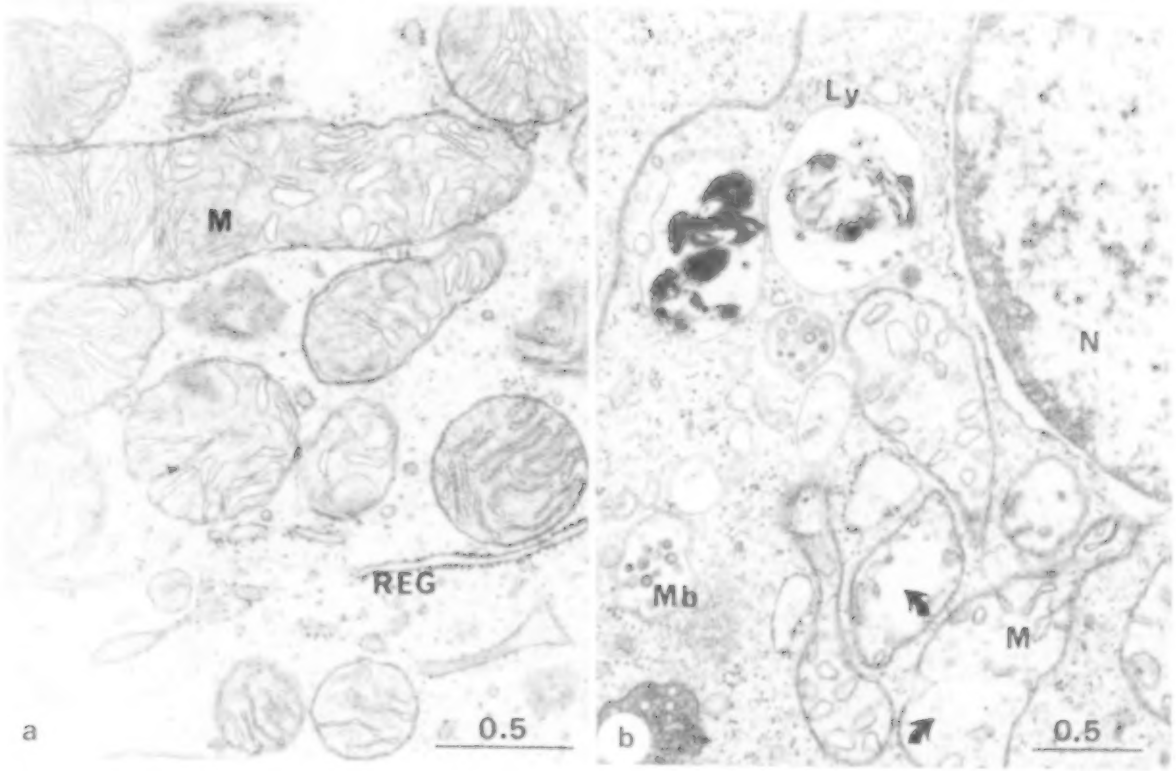
Fig. 8. (*a*) Mitochondria (M) in labial palp of *Macoma balthica*, control. REG, rough endoplasmic reticulum. (*b*) Labial palp of *M. balthica* from the Bay of Somme exposed to Cu. Note the lack of cristae (arrows) in mitochondria (M) and the needles (probably clay) in lysosomes (Ly). Mb, multivesicular bodies; N, nucleus. Scales bars in μm.



deposits of Ag, particularly in hemocytes (Martoja et al. 1988*a*). On the contrary, *M. balthica* exposed to 80 ng·mL^{-1} of Ag for 13 days showed rarely scattered microgranules in the basal lamina of the digestive gland alone (Amiard-Triquet et al. 1999). In the present study, the contaminated specimens exposed to 40 ng·mL^{-1} of Cu for 13 days contained scattered or aligned Cu-rich microgranules in the basal lamina and intercellular spaces of digestive gland, labial palps, and gills as well as in lysosomes of the digestive gland and in a few hemocytes.

The digestive gland and the gills are able to make endocytosis of aluminium silicate as clay. This phenomenon has been shown under natural conditions in another deposit-feeding bivalve, *Abra alba* (Martoja et al. 1988*b*), as well as in a filter-feeding bivalve, *C. gigas* (Jeantet et al. 1985). On the other hand, the labial palps are known to create a flow of alimentary particles. The presence of the endocytosed clay was unexpected in this organ and shows that labial palps are implicated here in mineral and nutriment absorption processes.

The presence of excess Cu in lysosomes of exposed specimens indicates that these organelles are able to play a role in detoxifying ions in excess in the medium through precipitation as shown in other bivalves (Jeantet et al. 1997). Basal lamina and intercellular spaces have already been described in other Molluscs as a site of mineral bioaccumulation of Cu. In particular, this was shown in the scallop, in the digestive gland of which Cu and Ag occur naturally (Ballan-Dufrançais et al. 1985). In the oyster, silver exposure is followed by an important deposit of silver sulfide coexisting with Cu in this tissular area (Martoja et al. 1988*a*). In *M. balthica*, after silver exposure, deposits of Ag and Cu occur in the basal spaces with S (Amiard-Triquet et al. 1999). In this experiment, intracellular concentrations of Cu were too low to determine the molecular form of Cu deposits. Nevertheless, the coexistence of S and Cu suggests that sulfur may be the chelating agent as shown previously in *Littorina littorea* (Martoja et al. 1980).

The existence of Cu and Zn in hemocytes has been described in *Ostrea edulis* (George et al. 1978). These two elements were sequestered independently: Zn in the type B amœbocytes (granular basophilic hemocytes described by Auffret 1989) and Cu in the type A amœbocytes (granular acidophilic hemocytes, Auffret 1989). In *C. gigas* exposed to cadmium in the metal-rich Gironde Estuary, France, we have found Cu and Zn in the granular acidophilic hemocytes (unpublished results). In the same species, after Ag exposure, hemocytes of granular basophilic type stored Ag_2S (Martoja et al. 1988*a*). In the present study, hemocytes appearing to be of the granular acidophilic type were able to store Cu when *M. balthica* was exposed to this element in excess.

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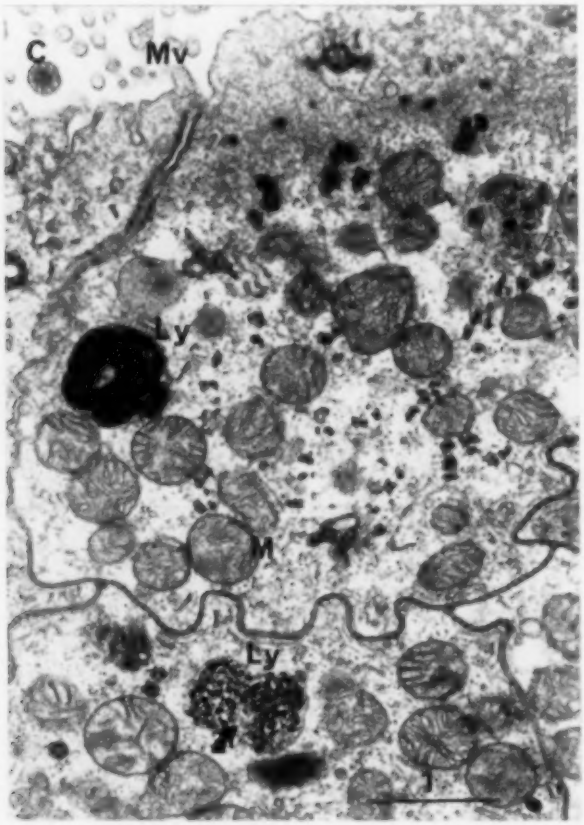

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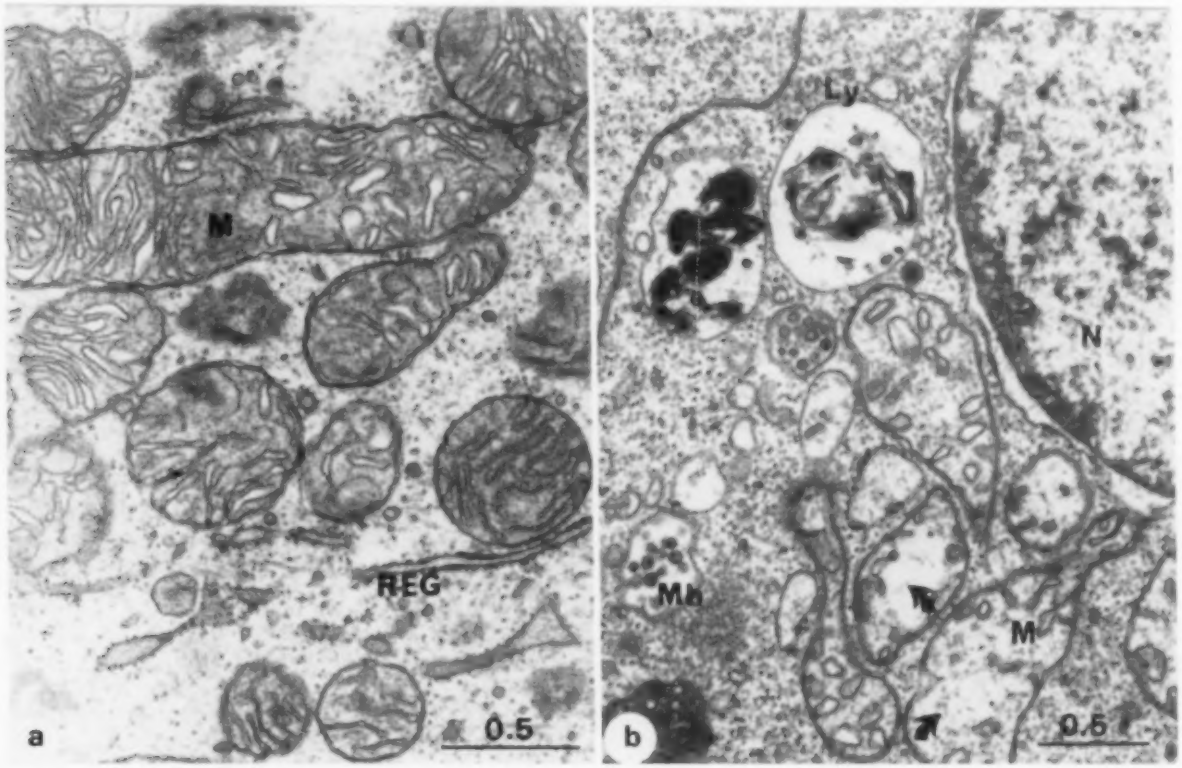

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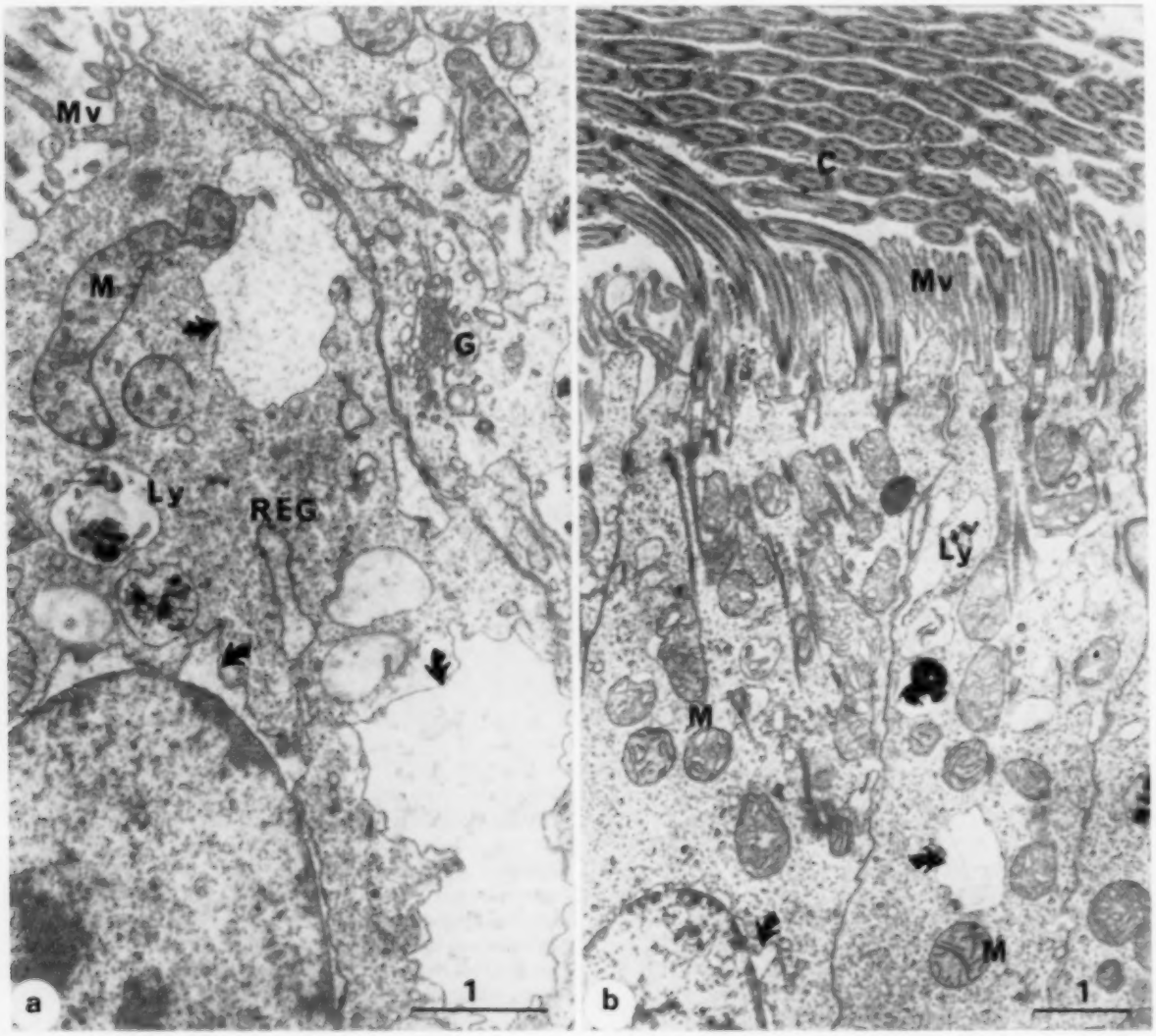

gesting that Cu concentration in Baltic clams was slowly regulated as a consequence of storage in fractions in which Cu turn-over was slow compared with that of Cu highly exchangeable in the cytosolic fraction. The presence of metals in such structures is generally considered as evidence for the deposits being involved in metal metabolism, and it is generally admitted that they have a role in metal detoxification (Mason and Jenkins 1995). This is in agreement with the findings of the present study showing few cytopathological effects in *M. balthica* exposed in the field (specimens from the Loire Estuary) or in the laboratory (specimens from both studied sites).

No significant relationship between Cu and MTLP levels was shown in clams from the Bay of Somme. In field studies, the importance of the latency for metallothionein induction has been underlined: for instance, Couillard et al. (1995) have estimated the response time of gill MT to the change in ambient Cd water to be 90 days. This length of exposure is very long compared with the period of exposure in the present study (13 days). However, the absence of MTLP level enhancement in specimens from the clean site is most probably independent of this factor. An experimental study has shown indeed an increase of MTLP levels in Baltic clams (*M. balthica*) exposed for only 2 days to a mixture of Cd, Cu, and Zn (Bordin et al. 1994). Contrary to what was observed in specimens originating from the Bay of Somme, a significant relationship between Cu and MTLP levels was shown in clams from the Loire Estuary. The possibility of a net MTLP increase in specimens from an industrialized site is an interesting result that has to be taken into account in

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the detoxifying processes of specimens living in a polluted area. Effectively, it seems that these clams could be then more able to detoxify by this way than those from a clean site. Moreover, *M. balthica* living in a metal-rich area are able to limit metal accumulation since we have shown that specimens originating from the industrialized site had accumulated significantly less Cu in their soft tissues when they were exposed to this element in their experimental medium. According to Mason and Jenkins (1995), limiting metal accumulation is one of the strategies adopted by marine organisms to prevent metal toxicity.

Adaptation processes allow the survival of *M. balthica*, which is a key species for the functioning of estuarine and coastal ecosystems, biologically rich but strongly impacted by human activities in Northwest Europe. However, it seems dangerous to relax water quality criteria on the assumption that all populations in polluted environments will evolve an increased resistance (Klerk and Weis 1987) since costs of tolerance have been evoked as maintenance of a tolerance mechanism may be energetically expensive (Postma et al. 1995 and literature cited therein). Moreover, species exhibiting high detoxification ability can constitute highly contaminated links in food chains. In *M. balthica*, about 35–38% of Cu is present in the cytosolic fraction of soft tissues, the latter being considered as the most easily available to predators (Amiard-Triquet et al. 1993; Reinfelder and Fisher 1994; Wang and Rainbow 2000 and literature cited therein).

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The authors thank Michel Duprez (GEMEL, St Valéry/Somme) for help in field work, the CME (Centre de microscopie électronique de l'IFR de Biologie Intégrative and the Service inter-universitaire Assistance à la Recherche, Université Pierre et Marie Curie, Paris, with the cooperation of Patricia Beaunier, and Anny Anglo and Lydia Massot for their technical help in preparing the samples for EPMA and electron microscopy.

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Diet of *Mysis relicta* in Lake Ontario as revealed by stable isotope and gut content analysis

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Abstract: Stable isotope analysis of the potential prey and predator can be combined with gut content analysis to quantify the diet. This dietary knowledge allows the quantitative assessment of the role of key species in energy and contaminant transfer, their impact on prey communities, and their susceptibility to perturbation. The diet of *Mysis relicta* was examined in Lake Ontario in spring, summer, and autumn using both techniques. Mysids fed on the bottom during the day and in the pelagia and on the bottom at night. A trophic fractionation of 2.2‰ N between mysids and their prey provided the best correspondence between the observed stable isotope signature of mysids and that estimated from their diet. Tissue turnover rate of $\delta^{13}C$ was slow compared with that of $\delta^{15}N$. Diatoms formed 50% of the assimilated diet in May. In September, 25% of large mysids feeding on the bottom contained amphipod parts and 20% contained phytoplankton. The remainder of the diet consisted of zooplankton and rotifers. The contribution of amphipods and phytoplankton could not be quantified. Revised daily consumption estimates, based on this new diet information and clearance rate estimates of consumption, gave daily consumption estimates similar to those estimated from previous bioenergetic modelling.

Résumé : L'analyse des isotopes stables chez les proies et les prédateurs potentiels combinée à l'examen des contenus du tube digestif permet de quantifier le régime alimentaire. Cette information rend possible l'évaluation quantitative du rôle des espèces-clés dans le transfert de l'énergie et des contaminants, de leur impact sur les communautés de proies et de leur vulnérabilité aux perturbations. Le régime alimentaire de *Mysis relicta* au lac Ontario au printemps, à l'été et en automne a été analysé à l'aide de ces deux techniques. Le jour, les *Mysis* se nourrissent sur le fond, mais la nuit ils s'alimentent à la fois dans les zones pélagique et profonde. Un fractionnement trophique de 2,2‰ de l'azote entre les *Mysis* et leurs proies donne la correspondance optimale entre la signature d'isotopes stables observée chez les *Mysis* et celle estimée à partir de leur régime alimentaire. Le taux de renouvellement tissulaire du $\delta^{13}C$ est faible par comparaison à celui du $\delta^{15}C$. Les diatomées constituent 50% de la nourriture assimilée en mai. En septembre, 25% des *Mysis* de grande taille à alimentation benthique ont des restes d'amphipodes dans leur tube digestif et 20% ont du phytoplancton. Le reste du régime alimentaire est composé de zooplancton et de rotifères. L'apport des amphipodes et du phytoplancton n'a pu être quantifié. Les taux révisés de consommation journalière, basés sur ces informations nouvelles et sur des estimations du taux de clearance de la consommation, donnent des estimaiions de consommation journalière semblables à celles obtenues à l'aide des modèles bioénergétiques antérieurs.

[Traduit par la Rédaction]

Introduction

The diet and feeding rates of mysids are of interest to quantitatively assess their role in energy and contaminant transfer, their impact on prey community structure and behaviour, and their susceptibility to the impact of exotics, such as *Bythotrephes*, *Cercopagis*, and *Dreissena*. The diets of mysids have traditionally been determined through the analysis of gut contents and enclosure feeding experiments. Gut content analysis has indicated that *Mysis relicta* is omnivorous, feeding on copepods, cladocerans, rotifers, algae (principally diatoms), benthos, and "detritus" (Grossnickle 1982). Estimates of feeding rates and selectivity coefficients for zooplankton prey have been determined in enclosure

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feeding experiments for *M. relicta* and related species (Bowers and Vanderploeg 1982; Nero and Sprules 1986; Mohammadian et al. 1997).

Mysis relicta migrates dielly, feeding in the upper part of the water column at night. Its vertical ascent is limited by temperature, light, and predator gradients (Gal et al. 1999; Rudstam et al. 1999). Mysids were thought to migrate to these waters because the opportunity to feed was much greater there than on the bottom of the lake. Several calculations on the impact of mysids on zooplankton have assumed that most of the caloric intake is from zooplankton (Murtaugh 1983; Rudstam et al. 1992; Gal 1999). Johannsson et al. (1994) tested the hypothesis that *M. relicta* in Lake Ontario feeds principally at night in the metalimnion. They compared the calories that a mysid could consume as it grew, given the feeding rates and selectivities of Bowers and Vanderploeg (1982) and Nero and Sprules (1986), and the caloric demand at observed growth rates calculated with the bioenergetics model of Rudstam (1989). The zooplankton food supply in the metalimnion was insufficient to support observed mysid growth through the winter and spring periods for all but the smallest mysids. In addition, adult females of the March cohort, the dominant cohort in the lake, could not meet their caloric requirements during the summer. Other sources of food and (or) significant food consumption during the day must occur to meet the calculated energy requirements or serious errors exist in the parameters of the bioenergetics model. The bioenergetics model has been validated in the laboratory using *M. mixta* (Gorokhova 1998) and performed well in matching mysid growth and consumption. Therefore, it is more likely that our understanding of the feeding ecology of *M. relicta* in Lake Ontario is incomplete.

Two possible sources of food that were not considered in the study of Johannsson et al. (1994) are diatoms and amphipods. Diatoms have often been observed in mysid guts (Grossnickle 1982), and significant feeding on phytoplankton has been documented for Lake Michigan mysids (Grossnickle 1979). Amphipods were caught and eaten by mysids in laboratory mesocosms (Parker 1980), and Green (1965) observed body parts that he thought might be amphipod remains in gut contents of mysids from Cayuga Lake, N.Y., U.S.A. Deepwater amphipods (*Diporeia hoyi*) normally burrow in the sediment, but a small proportion, generally <7%, swim up into the water column between April and August (Marzolf 1965). Amphipods may be susceptible to mysid predation at this time.

The relative ratios of stable isotopes of C (^{13}C and ^{12}C) and N (^{15}N and ^{14}N) in biota have been used in numerous studies as indicators of food source (Fry 1991). When combined with gut content analysis, stable isotopes may be used to assess the potential role of unidentifiable, undetectable, or unquantifiable prey in the diet. By combining the information in two recent studies, one on the Lake Ontario food web structure as mapped by stable isotopes and one on mysid diel feeding patterns based on gut content analysis, we examine the role of diel feeding patterns and other food sources in the diet of mysids in Lake Ontario and assess the potential of these sources to account for the lack of correspondence between caloric intake and caloric requirements noted above.

Methods and materials

The studies took place in the offshore of Lake Ontario, the most easterly of the Laurentian Great Lakes, in 1994 and 1995 at station 41 (130 m bottom depth, 28 km south of Cobourg) in concert with the Fisheries and Oceans Canada (Bioindex) long-term biological monitoring program.

Stable isotope study

Between April and October 1994 and 1995, the stable isotope signatures (SISs) ($\delta^{15}N$ and $\delta^{13}C$) of mysids >12 mm were determined monthly. The signatures of dominant zooplankton species and algal size fractions were determined every 2 weeks, except for a 6-week break through late August to the end of September in 1994, and less frequently in 1995. The signatures of *Diporeia* were measured on several occasions in the spring, summer, and fall of 1994 and 1995.

Mysids were caught in the water column at night with a 1-m^2 net with a 500-μm mesh cod-end. Mysids were also collected on occasion from the sediment surface using a benthic sled. Pelagic amphipods were collected from the mysid net samples in order to delineate any seasonal pattern in their presence in the water column. In August, September, and October 1995, a comparison was made of the SISs of ascending, descending, and benthic mysids as well as amongst small (<6 mm), medium (7–10 mm), and large (>12 mm) mysids. The October samples were collected further east in the main body of the lake off of Oswego. *Diporeia* were collected from the sediment with a Ponar grab. Zooplankton and algal size fractions were sampled during the day from the top 20 m of the water column or from the epilimnion (<20 m) when the water column was thermally stratified. Algae in the 20- to 64-μm size range were screened from a whole water sample. Zooplankton were collected with a 64-μm mesh net and passed through a series of mesh screens (110, 210, and 295 μm) to split the sample into smaller and larger size fractions. Individual species were later picked from the fractions. Each sample contained several thousand individuals. Zooplankton were collected separately from the epi-, meta-, and hypolimnion on 1 August 1995 in order to determine whether their SISs changed with the thermal layer.

All animals analyzed for stable isotopes were cleaned with distilled water or filtered, if necessary, and frozen (mysids, *Diporeia*, phytoplankton (particulate fraction) or preserved in 99.9% ethanol (zooplankton)). Acid was added to phytoplankton samples to remove carbonates. Samples were washed, picked, and dried at 60°C to get rid of any ethanol and water. Fluctuations in C signatures are more readily traced temporally when the influence of high lipid content is removed. Removal or loss of lipid will increase the $\delta^{13}C$ of the sample. Zooplankton lipid content was small, on the order of 1‰ or less and within the variability amongst composite samples, and was partially removed by ethanol preservation. *Diporeia* were lipid extracted prior to analysis, while the C signatures of mysids were lipid corrected afterwards using a relationship between the C/N ratio of *M. relicta* and their $\delta^{13}C$ signature (Leggett 1998). Neither method of preservation, followed by drying at 60°C, affects N SISs (Hobson et al. 1997; Leggett 1998; R.H. Hesslein, unpublished data). A Micromass continuous-flow isotope ratio mass spectrometer, fitted with a Carlo-Erba elemental analyzer as part of the inlet system (EA/CF-IRMS), was used to determine the $\delta^{13}C$ and $\delta^{15}N$ signatures. Analysis of standards of known isotope composition and duplicate analysis of the samples were used to assess the precision and accuracy of analysis within runs. The difference in $\delta^{13}C$ and $\delta^{15}N$ between duplicates and between standards and a known reference value was consistently 0.3‰ or less. Where sufficient mass (3–5 mg) was available, samples were also, or alternatively, analyzed using a VG-Optima EA-IRMS as a further check of measurement accuracy of the EA/CF-IRMS system. Continuous-flow instruments such as the EA/CF-IRMS rely on calibration

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against standards run consecutively to calculate isotope signatures of samples. In contrast, the VG-Optima EA-IRMS directly compares the ratio of isotopes in a sample to the ratio of isotopes in a standard of known isotopic composition.

Diet study

Samples for diet analyses were collected in May, August, and September. Mysids were collected from the bottom substrate with a benthic sled at the end of the day and again at the end of the night and from the water column with a mysid net just prior to dawn. In September, a daytime benthic sled sample was replaced by a dusk pelagic net sample as the mysids started their ascent. Mysids were preserved in 8% sugar formalin until analyzed. Twenty mysids >12 mm in length were measured and examined from each sample type. The mean (±1 SD) lengths of the mysids were 14.3 ± 1.4 mm in May, 15.4 ± 1.6 mm in August, and 13.6 ± 2.7 mm (descending), 15.1 ± 2.2 mm (benthic/day), and 16.3 ± 2.1 mm (benthic/night) in September. The contents of the gut were scored using a compound microscope, enumerating the number of *Limnocalanus*, other calanoids, cyclopoids, and cladoceran and rotifer species. Species identification was based on mandible, caudal appendage, and carapace/exoskeleton structure. Enumeration was based on the structure giving the highest animal count. Phytoplankton could not be quantified; therefore, the abundances of the dominant species were ranked on a scale from 1 to 4. The presence of larger organisms, such as watermites and amphipods, was noted but could not be enumerated. Only one watermite was seen. It was assumed that only one amphipod was consumed per individual mysid when amphipod remains were observed in the gut.

The biomass of prey consumed was calculated for each sample type and date. The mean number of each prey type eaten per mysid was multiplied by the mean weight of the prey. Average prey species biomass was obtained from hypo- and metalimnetic zooplankton samples collected during the same time periods by the Fisheries and Oceans Canada Bioindex program. We assumed that mysids ate 4-mm amphipods because an amphipod coxal plate found in the gut was 710 µm in length and would have come from a 4-mm amphipod.

A daily diet needed to be constructed before the relative contribution of nonquantifiable items could be assessed using stable isotopes. The diets from the three habitat/time periods (benthic/day, benthic/night, and pelagic/night) were significantly different in each of the three seasons (multivariate analysis of variance (MANOVA), $p < 0.001$). The diet described for each habitat/time period represents the relative contribution of different prey to the diet, not the total amount consumed during that habitat/time period. Therefore, the daily diet composition was constructed by averaging the diets from the three habitat/time periods, weighting for the proportion of the 24-h day the diet represented as well as the proportion of the mysid population found in the habitat type. At this point, diatoms could not be included because we had not been able to quantify their contribution; however, their relative abundance was noted so that their contribution could be estimated later using stable isotopes. The planktonic nighttime diet was given a weight of 0.9 of the nighttime time period and the benthic nighttime diet a weight of 0.1 of the nighttime time period. The ratio is an approximation, but we do know that most mysids feed in the water column at night, particularly in the summer and fall (Shea and Makarewicz 1989; Johannsson 1995). This procedure assumed that the gut contents from different habitat/time periods represented equal periods of feeding and that prey eaten in one time period will have passed out of the stomach by the end of the next time period when the mysids were sampled. It is unlikely that prey consumed during the day (or night) were counted as part of the diet during the following time period because the evacuation time of actively feeding mysids is generally on the order of 3–4 h at temperatures <10°C (Murtaugh 1984; Chipps 1998). In addition, our analysis requires evacuation of only the cardiac stomach, which is examined for gut content analysis, not the entire digestive tract.

Diatoms were the dominant phytoplankton group consumed. In order to determine their contribution to the mysid diet, the isotopic signatures of the dietary components needed to be brought into balance with the isotopic signature of the mysids, taking fractionation and C and N turnover times into consideration. The fractionation coefficient is a measure of the degree of change in the ratio of stable isotopes between trophic levels. We used the following equation, presented here for N isotopes:

$$(1) \qquad \delta^{15}N_M = (\delta^{15}N_h \cdot b_h/b_t + \delta^{15}N_i \cdot b_i/b_t + \delta^{15}N_j \cdot b_j/b_t + \ldots)$$

where $\delta^{15}N_M$ is the isotope signature of *M. relicta*, $\delta^{15}N_h$ is the isotope signature of the hth prey item plus the fractionation coefficient, and b_h/b_t is the proportion that h represents of the total biomass assimilated by *M. relicta*. Note that this analysis deals only with assimilated prey, not total prey consumed, and therefore assumes that mysids assimilated all quantified prey equally. As all quantifiable prey were animal matter and the vast majority were zooplankton, this assumption is not unreasonable. The possible contribution of nonquantified prey items to assimilated biomass can be assessed by including them in the equation.

We examined the correspondence between August calculated and observed mysid N SISs under a range of tissue turnover rates (0–100%) and levels of fractionation (1.8–3.0‰ in 0.4‰ steps) in order to parameterize these variables. August data were used because the diet was composed solely of quantifiable prey. Examination of turnover must consider the impact of new growth. In our assessment, all new growth was assumed to have the SIS of the diet corrected for isotopic fractionation. Percentage of new growth was determined by (*i*) estimating the length of the average mysid on the previous sampling date using a growth rate of 0.029 mm·day^{-1} for the April–September period and 0.012 mm·day^{-1} for the October–April period (Johannsson 1992), (*ii*) converting the initial and final length measurements to biomass using the equation developed for Lake Ontario mysids (Johannsson 1995):

$$(2) \qquad \ln(\text{weight(g)}) = -12.27 + 2.72 \ln(\text{length(mm)})$$

and (*iii*) expressing the difference in weight as a percentage of the final weight.

Results

Seasonal patterns in isotope signatures

No consistent differences were observed in either the C or the N signature of ascending, descending, and benthic mysids (Table 1). Therefore, stable isotope data from all habitats were combined to estimate the mysid SISs. The $\delta^{15}N$ signature increased with mysid size in the late summer and fall (ANOVA: $F = 19.63$, $p < 0.0001$). Similar increases in the $\delta^{15}N$ signature of mysids with size have been observed in Lakes Michigan, Huron, Champlain, and Memphremagog (Branstrator et al. 2000). Thus, the stable isotope and gut content data sets can legitimately be combined only for mysids of the same size range. Only data from larger mysids, comparable in size with those examined for gut content analysis, were used to establish the seasonal pattern in mysid SISs.

The $\delta^{13}C$ of *M. relicta* ranged between –26 and –28‰ with no distinct seasonal pattern (Fig. 1). The $\delta^{15}N$, on the other hand, followed a clear seasonal pattern, falling from between 12 and 13‰ in the spring to minimum values be-

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Table 1. Comparison of $\delta^{13}C$ and $\delta^{15}N$ of *M. relicta* separated by size and time and place of collection.

Sample type	*n*	$\delta^{15}N$	SD	$\delta^{13}C$	SD
Aug. 1995, station 41					
Small	5	8.61	0.69	–25.64	0.61
Medium	7	9.35	0.70	–26.80	0.37
Large	3*	9.60	0.16	–26.80	1.08
Sept. 1995, station 41					
Small	6	8.83	0.69	–26.09	0.42
Medium	4	10.45	0.40	–26.63	0.46
Large	3*	10.27	0.16	–26.84	0.41
Ascending	1*	9.98		–26.81	
Descending	1*	10.33		–26.72	
Benthic night	1*	10.11		–27.32	
Oct. 1995, Oswego					
Small	5	11.97	0.67	–24.75	1.02
Medium	5*	12.67	0.49	–25.24	0.30
Large	3*	13.35	0.49	–25.70	0.18
Ascending	1*	13.05		–25.82	
Descending	1*	13.08		–25.80	
Benthic night	1*	13.92		–25.49	

Note: Large (>12 mm), medium (7–10 mm), and small (<6 mm) mysids were collected from the pelagia. Ascending, descending, and benthic mysids were large individuals taken from the same samples as the mysids for gut content analysis. *n* is the number of samples analyzed.
*Composite of 20 individuals.

tween 9 and 11‰ in August (Fig. 1). The $\delta^{15}N$ values in the fall were close to 10‰.

The isotope signatures of the prey of *M. relicta* also showed seasonal patterns. The $\delta^{13}C$ of the amphipod *D. hoyi* ranged from –27 to –29‰ without seasonal pattern, while its $\delta^{15}N$ dropped from 13‰ in the spring to 10‰ by August and remained at that level through October (Fig. 1). The algal and zooplankton stable isotope data have been reported in companion papers by Leggett et al. (1999, 2000). The zooplankton data are key to the present study and the 1994 data are reproduced in Fig. 2 (redrawn from Leggett et al. (1999, 2000)). Data were collected more frequently in 1994 and have the same seasonal pattern as in 1995. In 1995, however, the copepod N signatures decreased earlier, in early June, as compared with early July. Limited data suggest that the $\delta^{15}N$ of some zooplankton species increased with depth in the water column during the stratified period (Table 2). The $\delta^{15}N$ and $\delta^{13}C$ of zooplankton from the meta- and hypolimnion were employed in the diet analysis for August. In September, the $\delta^{15}N$ and $\delta^{13}C$ of hypolimnetic *Limnocalanus* were used. Otherwise, the $\delta^{15}N$ and $\delta^{13}C$ of prey were taken from Fig. 2.

Diet

In the spring, the biomass of prey in mysid guts at the end of a day feeding on or near the bottom sediments was equivalent to that at the end of the night from mysids from pelagic samples (Table 3). *Limnocalanus* contributed the majority of enumerated biomass to the diet in the spring. Some differences in the diets did occur amongst the various habitat/time periods. Diatoms were more abundant in the guts of animals feeding on the bottom during the day than in animals feeding at night. Mysids also consumed more calanoids during the day near bottom and more cyclopoids at night in the water column.

During August, the pelagic diet afforded more biomass for the average mysid than benthic diet either in the day or in the night: 53 µg (pelagia) compared with 31 µg (daytime benthic) or 18 µg (nighttime benthic). *Bosmina* and cyclopoids were the dominant dietary items in the pelagia, and significantly more of these species were eaten per mysid feeding in the pelagia than feeding near the bottom (MANOVA, univariate *F* tests, Bonferroni corrected: $p \leq 0.007$). *Limnocalanus*, cyclopoids, *Bosmina*, and *Daphnia* were approximately of equal importance in the benthic diet. Diatoms were not seen in the guts at this time of year.

In the autumn, diatoms and chlorophytes were present in some guts but were not abundant. Most of the dietary biomass came from copepods in pelagic feeding mysids or amphipods in benthic feeding mysids. Thus, significantly more cyclopoids and rotifers were consumed by mysids at night in the pelagia than near the bottom during the night or day (MANOVA, univariate *F* tests, Bonferroni corrected: $p \leq 0.007$). Amphipods contributed a significant amount of biomass to the benthic diet, assuming that whole animals were consumed; however, they were eaten by only 10% of mysids during the day and 25% of benthic mysids during the night. If dead amphipods were partially eaten, their contribution could range greatly. The consumption of amphipods did not occur when amphipods were in the pelagia. Few amphipods were found off the bottom between August and October: <6% of the population was up in the water column between April and July during the three years for which we have data (1986, 1987, and 1995). In September, the nighttime benthic diet provided more biomass on average than the pelagic or daytime benthic diet, 80 µg compared with 54 and 40 µg, respectively, although success was skewed towards the few individuals that ate amphipods.

Stable isotopes can be used to estimate the consumption of prey items that are not easily quantified in normal gut analysis. It is a matter of balancing the mysid SIS calculated from the diet with that observed in the field. In order to calculate the expected mysid SISs from the diet, both the rate of tissue turnover of the isotopes and the degree of fractionation (enrichment) of the isotopes between the prey and the mysid need to be known. Carbon fractionation is normally <1‰ between trophic levels (Peterson and Fry 1987), which is within the variability of the data. Therefore, $\delta^{13}C$ fractionation was set to zero. Nitrogen fractionation is more variable. Nitrogen enrichment studies in the laboratory show a wide range of enrichment from –0.5 to 9.2‰ (DeNiro and Epstein 1981; Peterson and Fry 1987), although fractionation in natural populations often lies between 2 and 4‰ (Owens 1987; Toda and Wada 1990). The best correspondence occurred at 2.2‰ with 100% N tissue turnover (Table 4). Similar results could be obtained at 1.8‰ with 85% N turnover. Results deteriorated as fractionation increased above 2.2‰. As N fractionation is normally above 2‰, we conducted all further analyses using a N fractionation of 2.2‰.

In order to investigate the structure of the diet in the other seasons using stable isotopes, a series of assumptions were investigated sequentially. The first hypothesis stated that mysid tissue turnover times were faster than the shortest

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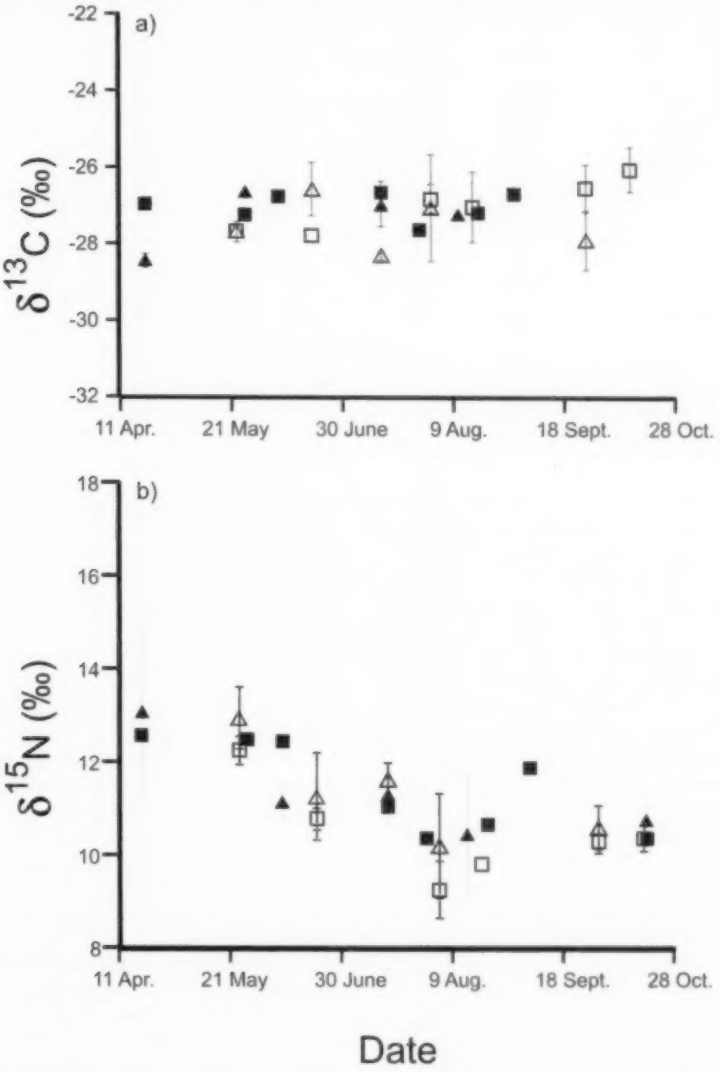
Fig. 1. Seasonal trends in (*a*) $\delta^{13}C$ and (*b*) $\delta^{15}N$ of *M. relicta* (lipid corrected) in 1994 (■) and 1995 (□) and *D. hoyi* in 1994 (▲) and 1995 (△) at station 41. Standard deviations are covered by the symbol if not visible.



intersampling interval and therefore that the tissue of the mysid should reflect solely the signature of its diet. The latter condition requires that the isotope signatures of prey items remain constant through one cycle of complete tissue turnover for N and C. The isotope signatures of the August dietary items, i.e. various zooplankton species, were stable from early June 1995 until the end of August 1995 (Fig. 2): gut contents were only measured in 1995. It was assumed that the May diet had also been stable for some time because processes are slow in the spring. However, the isotope signature ($\delta^{15}N$) of zooplankton increased between August and October. The transition was not documented, so it is not known whether the September mysids had been eating a diet principally of zooplankton with summer isotope signatures or whether the signatures had changed in September. Therefore, we investigated September scenarios assuming in the first instance that the dietary signature was the mean of the August and October signatures and in the second instance that the dietary signature reflected only summer zooplankton.

One further assumption had to be made: that all the mysids from a specific time period had the same feeding history. Mysids >12 mm in length can consume the same range of zooplankton species, from *Limnocalanus* to rotifers (Johannsson et al. 2001). These authors had no information on the diet of mysids between 9.5 and 11.9 mm in length. Mysids <9.5 mm did not contain *Limnocalanus*. This means that the smallest individuals measured for stable isotopes may not have included *Limnocalanus* in their diet to the same extent during the previous feeding period as depicted by the gut content analyses. This potential bias could overestimate the stable isotope contribution of *Limnocalanus* de-

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Table 2. Survey of the SISs of zooplankton collected from different depth strata in 1995.

	Date	$\delta^{13}C$	*n*	$\delta^{15}N$	*n*	C/N
Epilimnion						
Daphnia spp.	1 Aug.	–24.78	1	4.83	1	4.92
Bosmina spp.	1 Aug.	–24.77	1	4.56	1	4.33
Calanoid copepods	1 Aug.	–25.26	1	6.87	1	4.21
Diacyclops thomasi	1 Aug.	–24.37	1	8.30	1	
Diacyclops thomasi	1 Aug.	–23.10	1	8.93	1	4.02
Metalimnion						
Daphnia spp.	1 Aug.	–25.55	1	4.59	1	5.93
Bosmina spp.	1 Aug.	–23.55	1	5.70	1	3.68
Bosmina spp.	1 Aug.	–24.10	1	5.58	1	3.69
Calanoid copepods	1 Aug.	–24.64	1	8.51	1	
Diacyclops thomasi	1 Aug.	–23.27	1	10.24	1	
Hypolimnion						
Limnocalanus macrurus	1 Aug.	–26.01	2	11.82	2	4.62
Diacyclops thomasi	30 Aug.	–21.11	1	11.12	1	3.44
Limnocalanus macrurus	26 Sept.	–25.98±0.34	53	13.54±0.23	3	3.88±0.10

Note: *n* is the number of composite samples analyzed for stable isotopes.

rived from gut content analysis. The *Limnocalanus* portion of the diet ranged from 12.8% in September to 21% in August and 38.2% in May when diatoms were included. No bias would be expected in the spring when the N signature of *Limnocalanus* (20.6‰) was similar to that of the other dominant zooplankton in the diet (20.6–21.6‰). In August, few mysids occur in the 12-mm size range, and therefore, smaller mysids likely contributed little to the SIS measured at that time. In September, the N SIS of *Limnocalanus* was slightly higher than that of the other zooplankton and may have inflated the estimated N SIS based on the diet. But at this time of the year, *Limnocalanus* was only a small portion of the diet and the bias would have been within the range of sample error. If the *Limnocalanus* contribution was really 10% instead of 12.8%, the estimated N signature would be 0.07‰ lower, and if amphipods were removed from the calculations, it would be decreased by 0.1‰. Therefore, the analyses were not jeopardized by differential feeding histories in any season.

The theoretical $\delta^{15}N$ and $\delta^{13}C$ of mysids based on the daily diets from the three seasons, assuming 100% N and C turnover, did not accurately represent the actual isotope signatures of mysids collected at the same time (Table 5). In May, the C signatures were similar; however, the N signature of the diet calculated without diatoms (which were observed in quantities in the gut) was 19.9‰ compared with the mysid average of 12.2‰. In August, the $\delta^{15}N$ was similar (calculated as 9.9‰ and measured as 9.8‰), but the $\delta^{13}C$ suggested an alternative food source or lower rate of C turnover in the tissues (calculated as –24.6‰ but actually –26.5‰). In September, the dietary signature based on the mean signatures of the August and October prey was 13.3 and –24.8‰ and based on the summer prey signatures alone was 11.0 and –25.4‰ compared with measured mysid $\delta^{15}N$ and $\delta^{13}C$ of 10.3 and –27.2‰, respectively.

Our second hypothesis stated that mysid tissue N and C did not turn over rapidly, so that only the new growth would reflect the signature of the diet (Table 6). The percentage of new tissue was 57% in May, 31% in August, and 28% in September. Under the assumption of no tissue turnover, the $\delta^{13}C$ of mysids reflected the $\delta^{13}C$ of prey species available in May and August. In September, the $\delta^{13}C$ signatures of mysids were approximately 1‰ lower than that of their diet. It appears that C turned over very slowly in mysid tissue so that little or no effect could be observed between sampling dates, a maximum of 67 days between May and August. When tissue N was not allowed to turnover, the calculated $\delta^{15}N$ signatures of mysids did not correspond to observed values in May or August (Table 6).

Based on the results of the above analyses, we hypothesized that tissue N turned over completely, while tissue C did not turn over detectably during the intersampling periods. Given these assumptions, the calculated and observed isotopic signatures of mysids in August were essentially identical: 9.8 and –26.8‰ (observed) as compared with 9.9 and –26.6‰ (calculated). It appeared that N turned over more rapidly than C and that body tissue N had come into equilibrium with the prey. However, under these assumptions, discrepancies continued to exist between the measured and calculated $\delta^{15}N$ of *M. relicta* collected in May and September. Up to this point, diatoms were not included in the isotope mass balance of the diet of *M. relicta*, and amphipods were estimated to contribute 22.4% to the assimilated diet in September.

In May, large quantities of diatoms were consumed, while in September, small quantities of diatoms and green algae were eaten. Diatoms were estimated to have a $\delta^{15}N$ of 2–3‰ and a $\delta^{13}C$ of –29‰ in the spring (Leggett 1998). The proportion of the spring diet composed of diatoms was estimated by iteratively solving eq. 1 above to obtain the best match between calculated and observed mysid N signatures. If the spring diet were composed of 50–55% diatoms, the calculated mysid $\delta^{13}C$ signature would be within 0.4‰ of the observed signature (well within the range of sample variability) and the calculated $\delta^{15}N$ signature would bracket the observed $\delta^{15}N$.

The autumn data were much more difficult to reconcile because there were three variables: signature of the zooplankton prey, quantity of algae consumed, and the size (quantity) of amphipods eaten or scavenged. Summer zoo-

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Table 3. Diet of *M. relicta* in Lake Ontario at station 41, 1995, as determined by gut content analysis.

			Daytime benthic sled			Nighttime benthic sled			Nighttime pelagic net haul		
Month	Sample type	Prey dry weight	No. prey/ mysid	Weight/ mysid	% of diet	No. prey/ mysid	Weight/ mysid	% of diet	No. prey/ mysid	Weight/ mysid	% of diet
May	*Limnocalanus*	28.88	1.00	28.88	78.42	1.25	36.10	80.84	0.80	23.10	70.32
	Calanoid copepods	4.35	1.00	4.35	11.82	0.30	1.31	2.93	0.25	1.09	3.31
	Cyclopoid copepods	3.45	0.60	2.07	5.63	1.25	4.32	9.67	1.95	6.74	20.50
	Bosmina	1.88	0.80	1.50	4.07	1.50	2.81	6.30	0.80	1.50	4.57
	Eubosmina	1.90				0.05	0.10	0.21			
	Daphnia	3.80							0.10	0.38	1.16
	Keratella	0.01	0.05	0.00	0.00				0.10	0.00	0.00
	Kellicottia	0.01	0.35	0.00	0.01	1.05	0.01	0.02	1.35	0.01	0.04
	Notholca	0.04	0.45	0.02	0.05	0.35	0.01	0.03	0.80	0.03	0.10
	Tricocera	0.08									
	Amphipods	173.00									
	Total			**36.83**	**100.00**		**44.65**	**100**		**32.85**	**100**
	Diatoms*										
	Melosira		3.5			0.70			0.6		
	Cyclotella		2.6			0.45			0.3		
	Fragilaria		1.9			0.25			0.3		
	Tabellaria		2.7			0.35			0.3		
August	*Limnocalanus*	51.92	0.15	7.79	25.07	0.15	7.79	42.50	0.15	7.79	14.79
	Calanoid copepods	8.56	0.25	2.14	6.89	0.05	0.43	2.33	0.45	3.85	7.31
	Cyclopoid copepods	2.83	2.00	5.66	18.20	0.90	2.54	13.89	3.85	10.89	20.68
	Bosmina	0.70	7.85	5.52	17.78	5.95	4.19	22.85	31.75	22.34	42.43
	Eubosmina	1.93	0.05	0.10	0.31						
	Daphnia	3.33	2.95	9.82	31.61	1.00	3.33	18.16	2.25	7.49	14.22
	Keratella	0.01	1.45	0.01	0.05	3.05	0.03	0.17	18.60	0.19	0.35
	Kellicottia	0.01	1.60	0.02	0.05	1.15	0.01	0.06	11.20	0.11	0.21
	Notholca	0.04	0.35	0.01	0.05	0.20	0.01	0.04			
	Tricoceras	0.08									
	Amphipods	173.00									
	Total			**31.07**	**100**		**18.33**	**100**		**52.65**	**100**
September	*Limnocalanus*	48.93	0.10	4.89	12.28	0.10	4.89	6.14	0.16	7.73	14.28
	Calanoid copepods	8.46	0.70	5.92	14.86	1.65	13.96	17.53	2.53	21.38	39.51
	Cyclopoid copepods	1.39	2.25	3.12	7.83	3.90	5.41	6.79	7.21	10.00	18.47
	Bosmina	0.74	3.95	2.93	7.36	7.80	5.80	7.27	5.21	3.87	7.15
	Eubosmina	1.88	1.30	2.45	6.14	1.70	3.20	4.02	2.84	5.35	9.89
	Daphnia	1.93	1.65	3.18	7.99	1.60	3.09	3.88	2.84	5.49	10.14
	Keratella	0.01	1.85	0.02	0.05	3.05	0.03	0.04	8.74	0.09	0.16
	Kellicottia	0.01	0.25	0.00	0.01	0.45	0.00	0.01	2.26	0.02	0.04
	Notholca	0.04	0.05	0.00	0.01	0.10	0.00	0.01	0.05	0.00	0.00
	Tricocera	0.08	0.10	0.01	0.02	0.10	0.01	0.01	1.42	0.11	0.21
	Amphipods	173.00	0.10	17.30	43.40	0.25	43.25	54.28			
	Total			**39.82**	**100**		**79.64 (36.4†)**	**100**		**54.01**	**100**
	Algae*										
	Melosira					0.05			0.05		
	Cyclotella					0.05					
	Tabellaria								0.05		
	Staurastrum					0.15					

Note: Average prey weights were obtained by zooplankton net hauls in the hypo-, meta-, and epilimnion at the same time as the mysid samples. All weights are expressed in µg. No. prey/mysid, number of prey per mysid; Weight/mysid, weight of prey eaten per mysid.

*Abundance of dominant algal genera was ranked from 1 to 4 and is reported in the column "No. prey/mysid."

†Amphipods removed.

plankton SIS provided a better fit to the observed mysid $\delta^{15}N$ than the averaged August–October zooplankton SIS; however, the estimated $\delta^{15}N$ and $\delta^{13}C$ were still slightly too high (Table 6). Addition of a small amount of algae (5%) marginally improved the $\delta^{15}N$ and had no effect on $\delta^{13}C$. If mysids were scavenging amphipods, the fractionation of $\delta^{15}N$ by bacteria would enrich the amphipod tissue and exacerbate the difference between the dietary and observed $\delta^{15}N$ of mysids. If amphipods and algae were removed from the diet or contributed similar amounts to the assimilated diet, the estimated $\delta^{15}N$ from the diet would be close to the observed $\delta^{15}N$ of the mysids, 10.5 versus 10.3‰, respectively. The $\delta^{13}C$ still differed by 1.2‰.

Discussion

Stable isotope considerations

Stable isotopes are powerful but complex tools. To be

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Fig. 2. Seasonal trends in (*a*) $\delta^{13}C$ and (*b*) $\delta^{15}N$ of epilimnetic zooplankton collected at station 41 in 1994 and 1995. Redrawn from Leggett et al. (1999, 2000). D, *Diacyclops thomasi*; G, calanoids; B, *Bosmina*; C, *Daphnia*; R, rotifers. Uppercase letters are 1994 data and lowercase letters are 1995 data.

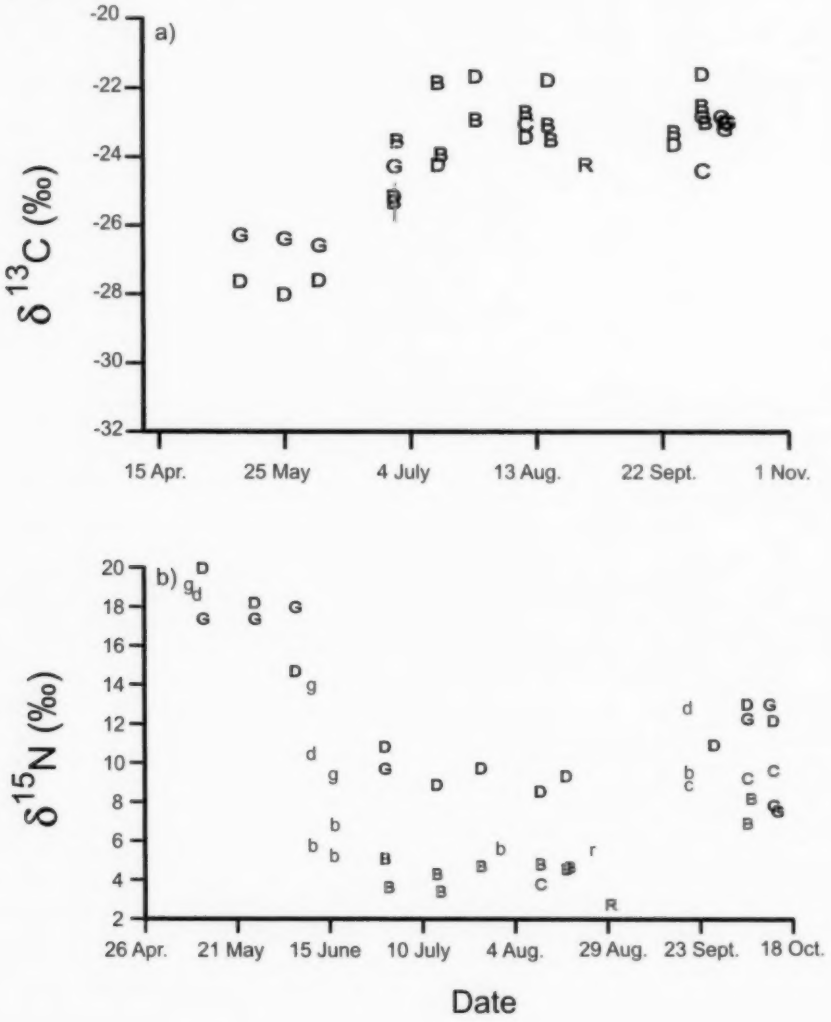

Table 4. Calculated August mysid SISs were determined from gut content analysis, as they were affected by the level of N fractionation and tissue N turnover rates.

	Level of N fractionation			
N turnover in old tissue	1.8‰	2.2‰	2.6‰	3.0‰
0% N turnover	11.3	11.5	11.6	11.7
100% N turnover	9.5	**9.9**	10.3	10.8
85% N turnover	**9.8**			
Mysis relicta (actual N signature)	**9.8**	**9.8**	**9.8**	**9.8**

Note: Growth from May until August resulted in 33% new tissue. Conditions of best agreement with observed mysid SIS are bolded. See Methods and materials for more details.

used effectively in diet analysis, they need to be combined with knowledge of the seasonal changes in isotopic signatures of prey species, the level of enrichment specific to the predator in its environment, and the turnover rates of the stable isotopes in the predator. We determined the seasonal pattern of isotopic signatures in the prey species; however, we had to make assumptions concerning the level of enrichment and rates of turnover. The fractionation factors and turnover rates were determined empirically and fell within the range of previously published values (e.g. Owens 1987; Peterson and Fry 1987; Toda and Wada 1990). The best correspondences between the theoretical and actual mysid SISs were obtained under the assumptions that N enrichment was 2.2‰ for all prey, the rate of C turnover was essentially zero, and the rate of N turnover was more rapid, the tissue N being completely replaced within the intersampling period. Good correspondence could also be obtained at lowered levels of enrichment if N turnover was slower. We worked with 2.2‰ because it fell closer to the range of normally observed values. These results suggest that changes in diets are

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Table 5. Dietary analysis of *M. relicta*.

Date		% of identifiable gut contents	$\delta^{15}N$ of food item + 2.2‰	$\delta^{13}C$ of food item + 0‰	Contribution to *M. relicta* $\delta^{15}N$	Contribution to *M. relicta* $\delta^{13}C$
23 May 1995	*Limnocalanus*	76.3	20.6	–28.0	15.7	–21.4
	Calanoid copepods	9.1	20.6	–27.0	1.9	–2.5
	Cyclopoid copepods	9.9	21.6	–28.0	2.1	–2.8
	Cladocerans	4.6	5.1	–28.0	0.2	–1.3
	Rotifers	0.1	6.1	–23.0	0.0	0.0
	Mysis relicta (from gut contents)				19.9	–28.0
	Mysis relicta (actual)				12.2	–27.5
1 Aug. 1995	*Limnocalanus*	21.0	14.1	–26.0	3.0	–5.5
	Calanoid copepods	7.0	10.7	–24.6	0.7	–1.7
	Cyclopoid copepods	19.2	12.3	–23.3	2.4	–4.5
	Daphnia	24.0	6.8	–25.6	1.6	–6.1
	Bosmina	28.5	7.8	–23.8	2.2	–6.8
	Rotifers	0.3	6.1	–23.0	0.0	–0.1
	Mysis relicta (from gut contents)				9.9	–24.7
	Mysis relicta (actual)				9.8	–26.5
			Mean (Aug. and Oct.) prey signatures			
25 Sept. 1995	*Limnocalanus*	12.8	14.7	–26.0	1.9	–3.3
	Calanoid copepods	27.5	14.2	–22.5	3.9	–6.2
	Cyclopoid copepods	13.1	14.2	–22.8	1.9	–3.0
	Daphnia	8.7	12.1	–25.9	1.1	–2.3
	Bosmina	7.3	10.2	–23.6	0.7	–1.7
	Eubosmina	7.9	11.2	–24.8	0.9	–2.0
	Rotifers	0.3	6.1	–23.0	0.0	–0.1
	Amphipods	22.4	13.0	–28.0	2.9	–6.3
	Mysis relicta (from gut contents)				13.3	–24.9
	Mysis relicta (actual)				10.3	–27.2
			Summer prey signatures			
25 Sept. 1995	*Limnocalanus*	12.8	14.1	–26.0	1.8	–3.3
	Calanoid copepods	27.5	10.7	–24.6	2.9	–6.8
	Cyclopoid copepods	13.1	12.3	–23.3	1.6	–3.1
	Daphnia	8.7	6.8	–25.6	0.6	–2.2
	Bosmina	7.3	7.8	–23.8	0.6	–1.7
	Eubosmina	7.9	7.3	–24.7	0.6	–1.9
	Rotifers	0.3	6.1	–23.0	0.0	–0.1
	Amphipods	22.4	13.0	–28.0	2.9	–6.3
	Mysis relicta (from gut contents)				11.0	–25.4
	Mysis relicta (actual)				10.3	–27.2

Note: The contribution to the overall $\delta^{13}C$ and $\delta^{15}N$ of *M. relicta* was calculated based on the apportionment of diet from gut content analysis. See text for details of diet and apportionment. This theoretical value is compared with the observed $\delta^{13}C$ and $\delta^{15}N$ values of *M. relicta*. Rotifer SIS was only measured in the summer: these values were applied in May and September.

more rapidly reflected in $\delta^{15}N$ than in $\delta^{13}C$. The C turnover rate appears to be exceedingly low. Gorokhova and Hansson (1999) found that the $\delta^{13}C$ signature of *M. mixta* muscle tissue, which forms the bulk of the mysid signature, changed by half the difference between the original muscle SIS and that of their prey when *M. mixta* doubled their weight. This could only occur if the muscle tissue C turnover rate was insignificant (essentially zero). With respect to N turnover, similar rates were observed by Hesslein et al. (1993) for whitefish and by Gorokhova and Hansson (1999) for *M. mixta*.

Assessment of mysid consumption model

Stable isotope assessment of the diet indicated that a large proportion of the spring diet and a smaller portion of the autumn diet consisted of nonquantified prey with a low $\delta^{15}N$ signature. These missing dietary components were likely composed of diatoms (spring), diatoms, chlorophytes, and amphipods (autumn), and copepod nauplii. Large quantities of diatoms were observed in the guts in May. The $\delta^{15}N$ signature of diatoms was much lower than the signatures of the zooplankton prey. Copepods likely fed mainly on younger instars during the winter. Growth is important to copepods at this time because many reach maturity over the winter and reproduce in the early spring. Mysids grow slowly over the winter, with growth increasing in the early spring. Much of their growth likely occurred while diatoms were abundant and copepods highly enriched with N. If the assimilated diet were composed of 50–55% diatoms, the $\delta^{15}N$ and $\delta^{13}C$ signatures of May mysids would be reconciled with their diet.

Removal of amphipods improved the correspondence of the September diet and mysid signature; however, amphi-

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Table 6. Actual and calculated SISs of *M. relicta* from Lake Ontario, station 41, 1995.

Month	Condition	*Mysis relicta* $\delta^{15}N$	*Mysis relicta* $\delta^{13}C$	*Mysis relicta* $\delta^{15}N$	*Mysis relicta* $\delta^{13}C$
May	*Mysis relicta* (actual)	12.2	–27.5		
	Diet from gut contents	20.0	–27.9		
	No turnover of C and N in tissue	15.8	–27.6		
	Total N turnover, no C turnover	20.1	–27.6		
	If 50–55% of assimilated diet were diatoms	**12.5–11.8**	**–27.9**		
Aug.	*Mysis relicta* (actual)	9.8	–26.5		
	Diet from gut contents	9.9	–24.7		
	No turnover of C and N in tissue	11.5	–26.6		
	Total N turnover, no C turnover	**9.9**	**–26.8**		
		(Aug. + Oct.)/2 prey SIS		Summer prey SIS	
Sept.	*Mysis relicta* (actual)	10.3	–27.2	10.3	–27.2
	Diet from gut contents	13.3	–24.9	11.0	–25.4
	No turnover of C and N in tissue	10.9	–26.0	**10.3**	**–26.2**
	Total N turnover, no C turnover	13.3	–26.0	11.0	–26.2
	Total N turnover, no C turnover, plus 5% algae	12.9	–26.0	10.9	–26.2
	Total N turnover, no C turnover, no amphipods or algae	13.3	–25.8	**10.5**	**–26.0**

Note: Signatures were calculated from gut content analyses under different scenarios of tissue turnover rates and addition of diatoms, which were observed in the guts in May and to a small extent in September but were not quantified. The bolded scenarios come closest to matching observed mysid signatures. N fractionation was 2.2‰. Percentage of new tissue growth during September–May, May–August, and August–September was 60, 33, and 30%, respectively.

pods and algae were consumed in the fall. The N SIS of amphipods and algae bracketed the observed SIS of mysids at this time and equal contributions of these two groups to the assimilated diet tended to cancel out each other. Algae were observed in only 10% of all mysids analyzed in September, and then only in small quantities, suggesting that amphipods also contributed little to the total diet. If amphipods and (or) algae were a seasonal component only added to the diet in the fall, the SIS of mysids would not yet have reached equilibrium with the SIS of these prey. In that case, we may be underestimating the importance of amphipods to the diet.

Unfortunately, we do not have information on the isotopic signature of nauplii. Nor were they seen in the diet because they disintegrate very rapidly (Rudstam et al. 1989). However, they were clearly eaten by mysids in feeding experiments conducted at the same time (O.E. Johannsson, unpublished data). Clearance rate calculations on metalimnetic naupliar densities suggest that nauplii could form 16% of the zooplankton biomass consumed at night in the pelagia in May, <1% in August, and 1% in September (data from calculations in Johannsson et al. 1994). Thus, naupliar consumption would not affect the results of our analysis in August or September but may be important in the spring.

The daily caloric intake estimated by Johannsson et al. (1994) for Lake Ontario mysids, using clearance rates, assumed that all feeding occurred in the metalimnion at night and that the diet was restricted to zooplankton prey. Mysids could not acquire sufficient calories to maintain observed growth rates under these conditions. Caloric consumption of mysids in Johannsson et al. (1994) can be reassessed by combining our new information on the quantitative importance of phytoplankton in the diet and daily patterns of food intake with the calories consumed by a mysid feeding solely on zooplankton at night. In the spring, mysids feed during the day as well as the night; nighttime consumption over 8 h can be corrected to a 24-h basis by multiplying by 3. The calories consumed can be doubled to account for the diatom input to the assimilated diet. Therefore, the actual caloric intake of a mysid should be in the vicinity of six times that estimated from nighttime clearance rates on zooplankton in the spring. This new estimate of dietary intake would provide sufficient calories for all mysids except the very large females of the August cohort (cf. fig. 2 in Johannsson et al. 1994). In August, mysids depend principally on feeding on zooplankton at night in the pelagia: stable isotope analysis did not indicate that any prey type was missing from the diet, and the guts contained more prey biomass after feeding in the pelagia than at any other time. We assumed that the composition of the daily diet could be estimated by combining the diets from the different habitat/feeding periods, weighting only for the time of feeding in that habitat and proportion of the population inhabiting that habitat. This implicitly assumes that the rate of feeding is proportional to the amount of prey biomass in the gut. These assumptions would imply that the total diet in August was 2.2 times larger than the nighttime diet alone. If the clearance rate estimates of consumption were multiplied by 2.2, all but the largest mysid could obtain sufficient calories to sustain observed growth even at the lower clearance rates of Nero and Sprules (1986) (cf. fig. 2 in Johannsson et al. 1994). In September, these assumptions were applied to the diet after amphipods were removed and then the daily diet was increased by 10% to account for the consumption of algae and amphipods. The total daily diet was close to two times the nighttime clearance rate estimates. Again, this level of consumption would supply sufficient calories for all but the largest mysids.

The caloric requirement of larger females exceeded the daily diet estimates of caloric consumption in all time periods. The clearance rate estimates used by Johannsson et al. (1994) were based on the average of a group of mysids 14–

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17 mm in length (Bowers and Vanderploeg 1982) and 12–14 mm in length (antenal scale length converted to total body length using fig. 2 of Grossnickle and Beeton (1979)) (Nero and Sprules 1986). Clearance rate increases with mysid size (Murtaugh 1983). Thus, the clearance rates of the largest females were likely underestimated by Johannsson et al. (1994).

Diet

Mysis relicta is an opportunistic omnivore. Dietary evidence from Char and perhaps Cayuga lakes attests to its ability to feed on organisms that live on or near the bottom (Green 1965; Lasenby and Langford 1973). Other omnivorous, migrating mysids have also demonstrated an ability to feed near or on the sediment surface: *M. mixta* (Rudstam et al. 1989) and *Neomysis mercedis* (Siegfried and Kopache 1980; Johnston and Lasenby 1982). Evidence for daytime and nighttime benthic feeding by *M. relicta* in Lake Ontario comes from two observations. First, spring diets were significantly different between habitats and times of day without a change in total quantifiable prey biomass in the guts. In the spring, animals on the bottom contained more diatoms and calanoids and fewer cyclopoids than animals that feed in the pelagia. Second, in September, bottom-dwelling mysids consumed amphipods, particularly during the night. The consumption of amphipods by mysids had been documented before in laboratory microcosms (Parker 1980). As mysids fed on amphipods in the autumn, they were not feeding on amphipods when amphipods were maximally abundant in the water column but when these prey were on or near the sediment surface. Juvenile amphipods recruit to the population in September in mid-Lake Ontario and amphipod densities reach their peak at this time (Johannsson et al. 1985). Increased densities may increase the potential for predation on amphipods by mysids.

Observations on the seasonal availability of mysids to capture by vertical net hauls suggest that the relative value of benthic and pelagic nighttime diets may affect the vertical distribution of mysids. Johannsson (1995) studied the abundance, distribution, and production of the entire population of mysids in Lake Ontario for a 1-year period. She found that the abundances of all size-classes of mysids caught in May were lower than those caught in July or October. Differences in abundance could not be accounted for by recruitment and (or) growth. This same observation had been made repeatedly at station 41 during the Bioindex open-lake monitoring program (Johannsson 1992). In May, the mass of zooplankton prey in the guts of pelagic and bottom-feeding mysids at night was similar and diatoms were more abundant in benthic feeding mysids. There was no obvious feeding advantage to a mysid to migrate up into the pelagia to feed. In August, however, gut contents indicated that it was much more advantageous to feed in the surface waters than to feed near the bottom. The same was true in September, except perhaps for a few mysids that caught amphipods. Therefore, a larger proportion of the mysid population may be in the pelagia at night during the summer and autumn months than during the spring.

In conclusion, the marriage of gut content analysis and stable isotope data has provided a strong framework for developing and assessing our knowledge of animal diets. Through this two-pronged approach, we have demonstrated the quantitative importance of diatoms to the mysid diet in the spring in Lake Ontario and improved our understanding of the relative importance of pelagic and benthic feeding to the mysid diet through the season. With the inclusion of diatoms in the spring diet and benthic feeding in all seasons, we have been able to account for the calories required to support mysid growth in Lake Ontario as determined by bioenergetic modelling. These results confirm the general importance of the diatom and deep zooplankton/benthic pathways of energy flow in supporting the mysid population. According to our estimates, they can account for approximately half the caloric requirements of the mysid population. Mysids function as an important intermediary, funneling energy from several pathways to the fish community. Because mysids are a broad conduit, they may dampen fluctuations in energy flow within individual pathways, helping to stabilize the fish community. Given the lack of diversity in medium-sized deepwater invertebrates in the Great Lakes, the flexibility in diet exhibited by mysids is not only beneficial for the mysid population but also good for the ecosystem.

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Estimating in-river survival of migrating salmonid smolts using radiotelemetry

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Abstract: A field study to estimate the survival of outmigrating steelhead (*Oncorhynchus mykiss*) smolts using radiotelemetry methods is illustrated. A paired release–recapture design was used to estimate pool (i.e., reservoir), dam, and project (i.e., reservoir plus dam) survival at two mid-Columbia River hydroprojects based on maximum likelihood estimation. The release and detection scheme was designed to minimize the possibility of detecting false-positive radio signals from smolts that might have died upstream during the hydroproject passage. Model assumptions and possible violations are discussed. Releases of radio-tagged and passive integrated transponder (PIT) tagged steelhead smolts were also compared to assess the possible effects of tag type on migration behavior. Survival through the Rocky Reach project (P = 0.86) and Rock Island project (P = 0.41) and bypass diversion probabilities at Rocky Reach Dam (P = 0.39) were found to be similar between tag types. Small but significant differences in arrival patterns (P = 0.02) and travel times (P = 0.01) were observed between radio-tagged and PIT-tagged smolts.

Résumé : On trouvera ici la description d'une étude de terrain qui cherche à estimer à l'aide de la télémétrie la survie de saumoneaux de la Truite arc-en-ciel anadrome (*Onchorhynchus mykiss*) qui retournent à la mer. Un plan de relâchement–recapture apparié a servi à estimer, à l'aide d'une estimation de vraisemblance maximale, la survie dans les profonds (i.e., le réservoir), le barrage et la structure complète (i.e., le réservoir et le barrage) aux sites de deux projets hydroélectriques dans le cours moyen du Columbia. Les plans de relâchement et de détection étaient prévus pour minimiser la possibilité de détecter des radio-signaux faussement positifs provenant de saumoneaux morts en amont en traversant l'ouvrage hydroélectrique. Les présuppositions du modèles et leurs violations possibles font l'objet d'une discussion. La comparaison de relâchements de saumoneaux munis d'un radio-émetteur et d'autres porteurs de PIT (transpondeur passif intégré) a permis d'évaluer les effets possibles du type d'émetteur sur le comportement migratoire. La survie à travers l'ouvrage de Rocky Reach (P = 0,86) et celui de Rock Island (P = 0,41) et la probabilité de diversion dans la dérivation du barrage de Rock Reach (P = 0,39) étaient les mêmes pour les poissons munis des deux types d'émetteurs. De petites différences significatives pouvaient cependant s'observer dans les patterns d'arrivée (P = 0,02) et les temps de déplacement (P = 0,01) entre les saumoneaux porteurs des deux types d'appareil.

[Traduit par la Rédaction]

Introduction

The increasing number of salmonids listed under the U.S. Endangered Species Act (ESA 1973) in the Pacific Northwest has prompted the need for flexible and precise methods of estimating survival rates of outmigrating smolts. The need for precise monitoring and evaluating data from mitigation programs is counterbalanced by the strict limitations for handling and studying endangered stocks under the ESA. In the past, PIT (passive integrated transponder) tags have provided a precise and reliable means of generating smolt survival estimates in the Columbia River Basin (Skalski et al. 1998). However, often tens of thousands of tagged smolt are needed to obtain precise estimates of survival. The purpose of this paper is to present the adaptation of release–recapture methods to radio-tag studies for the purposes of estimating smolt survival. The developments of miniaturized radio tags, high downstream detection rates, and new statistical models hold the promise of providing both precise and more detailed survival information with vastly fewer tagged fish at a time when informational needs are increasing (e.g., 90 000 PIT-tagged smolts versus 500 radio-tagged smolts at Rock Island project in 1999).

Release–recapture models for estimating survival probabilities of tagged animals have been available since the formative work of Cormack (1964), Jolly (1965), and Seber (1965). Burnham et al. (1987) adapted these methods specifically for estimating smolt survival through hydroprojects. More recent efforts have been focused on modeling survival relationships using tagging data (North and Morgan 1979; Lebreton et al. 1992; Skalski et al. 1993). In all of these

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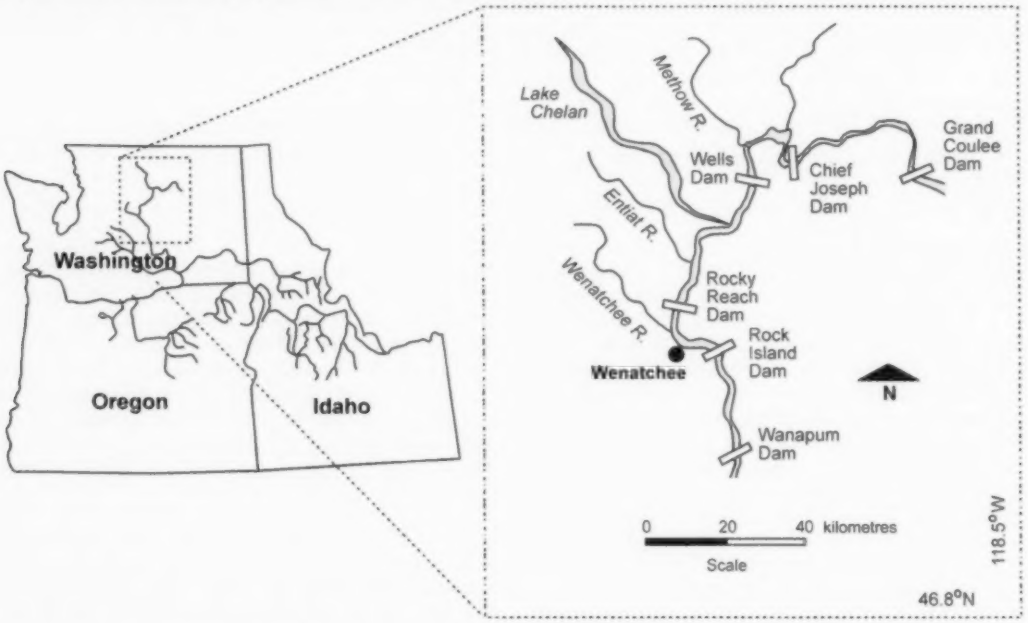
Fig. 1. Study area for the survival study conducted in mid-Columbia River, Washington, U.S.A., 1999.



methods, the statistical models are based on the recapture or detection of live individuals. However, with the use of radio tags, radio signals may be received even after a smolt has died. For this reason, field methods for releasing and detecting radio-tagged smolts must be modified along with the statistical models to assure valid survival estimates.

This paper describes the logistical requirements for performing smolt survival studies during outmigration using radiotelemetry, the statistical models for estimating survival through pools (i.e., reservoirs), dams, and projects (i.e., reservoir plus dam), and an assessment of radio-tag effects on migration behavior. General principles for the conduct and analysis of radiotelemetry smolt survival studies will be presented.

Materials and methods

Study area

The study methods and analysis for a radio-tag survival study were assessed in the mid-Columbia River (Fig. 1) from the tailrace of Wells Dam (river kilometre (RK) 830.1) to the forebay of Wanapum Dam (RK 669.2). Within that reach, two hydroprojects, the Rocky Reach Dam (RK 762.3) and the Rock Island Dam (RK 729.7), operated by the Chelan County Public Utility District No. 1 reside. The objective of the survival study was to estimate project survival and to partition project survival into the components of reservoir and dam passage survival at those two hydroprojects.

Rocky Reach Dam is located on the Columbia River approximately 11 km upstream of the city of Wenatchee, Washington. The project consists of a single powerhouse oriented parallel to the river flow with a total of 11 turbine units, each having three intakes. The spillway is perpendicular to the river flow and has a total of 12 spillbays. The dam has two prototype surface collector entrances and bar screen deflectors combined with a gatewell collection system in turbine units 1 and 2 for juvenile salmonid passage. Radio-antenna systems were deployed throughout all possible passage routes of this dam complex. The ability to tailor radiotelemetry detection equipment to the site-specific requirements of a site is an advantage of the radio-tag methodology. The reservoir extends to Wells Dam and is 66 km in length.

Rock Island Dam is located approximately 21 km downstream of Wenatchee, Washington. The dam has two powerhouses. The original powerhouse No. 1, built in 1933, has 10 vertical-axis turbine units, each with three intakes. Powerhouse No. 2, built in 1979, has eight horizontal-axis turbine units, each with two intakes. The spillway consists of 32 spillbays separated between bays 14 and 16 by an adult fish ladder. The reservoir extends to Rocky Reach Dam 32 km upstream.

The downstream detection site for the study was at Wanapum Dam, approximately 5 km downstream of the town of Vantage, Washington. The reservoir between Rock Island and Wanapum dams is 60 km in length.

Radio transmitters

The radiotelemetry tags used in this study were pulse-coded transmitters developed by Lotek Engineering Co. of Newmarket, Ont., Canada. The tags, model MCFT-3GM, were 8.2 mm in diameter and 18.9 mm in length and weighed 1.75 g in air and 1.4 g in water. The in-water weight of the tag is the more important measure for it best characterizes the added burden of the tag on the fish. The tags were powered by a 3.0 V battery that provided a reported minimum tag life of 22 days at the prescribed transmission rate of one pulse every 2.5 s. Stainless steel, 40-cm-long antennas were used on the tags.

System antenna configuration

Radio-tagged smolts were monitored at Rocky Reach, Rock Island, and Wanapum dams during the downstream migration. At each dam, two independent antenna–receiver systems were deployed. The primary system at each dam consisted of four-element aerial antennas distributed across the upstream face of the structure along the deck. At Rocky Reach, seven aerial antennas were deployed along the upstream face of the spillway, with one antenna at

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Table 1. Summary of the deployment for antennas used in the 1999 radiotelemetry study at Chelan County Public Utility District.

		Number of antennas	
Dam	System	Spillway	Powerhouse(s)
Rocky Reach	Primary–aerial	7	11
	Secondary–underwater	16	84
Rock Island	Primary–aerial	12	8 (PH#1), 5 (PH#2)
	Secondary–underwater	43	64 (PH#1), 32 (PH#2)
Wanapum	Primary–aerial	9	8
	Secondary–aerial	9	8

each of spillbays 2–8 (spillbay 1 was closed during the study). Eleven aerial antennas were deployed along the upstream edge of the Rocky Reach powerhouse, one at each of turbine units 1–11. At Rock Island Dam, eight aerial antennas were evenly spaced (30.5 m) across the upstream face of powerhouse No. 1. Similarly, five aerial antennas were spaced 30.5 m apart across the upstream face of powerhouse No. 2. Another 12 aerial antennas were evenly spaced (30.5 m) across the breadth of Rock Island spillway.

At Rocky Reach and Rock Island dams, the secondary antenna systems consisted of underwater antennas deployed throughout each of the passage locations (i.e., powerhouse, spillway, and bypass system). For the powerhouses at each project, two underwater antennas were mounted within the individual headgate slots of each turbine intake. At the spillways, underwater antennas were mounted to the pier nose of each spillbay. At Rocky Reach Dam, this consisted of two antennas within each spillbay. At Rock Island, some of the spillbays were capable of spilling water near the surface and from the bottom simultaneously; in which case, four antennas were deployed per spillbay.

At Wanapum Dam, both primary and secondary systems consisted of four-element aerial antennas connected to separate independent receivers. Each aerial antenna system was composed of 17 aerial antennas evenly spaced across the breadth of the project. Table 1 summarizes the antenna deployment used in the study at the various hydroprojects.

For all aerial systems, radio receivers (SRX model manufactured by Lotek Engineering Co.) were used with a scan period of 3 s. Multiple receivers were used to minimize the number of channels monitored by each receiver. Underwater antenna arrays were monitored by SRX/Digital Spectrum Processor (DSP) systems. These DSP systems allowed all antennas and frequencies to be monitored simultaneously. Details of the antenna arrays and receiver configuration can be found in Stevenson et al. (2000).

Fish tagging and release

To estimate survival through the pools and dams at Rocky Reach and Rock Island, a total of approximately 250 run-of-river steelhead (*Oncorhynchus mykiss*) smolts were tagged and released in each at the tailraces of Wells, Rocky Reach, and Rock Island dams during 10 releases of 25 fish at each release site over a 12-day period. Data were pooled in the subsequent survival analyses.

To assess potential behavioral effects associated with radio-tag implantation, an additional 508 run-of-river steelhead were tagged with 134.2 kHz PIT tags and released over the same 12-day period and concurrent with the radio-tagged smolt releases at Wells tailrace (i.e., 10 releases of 50 smolts each). In this comparative study, PIT-tagged fish were considered to be the reference group for comparison with the more invasively tagged radio-tagged fish. These concurrent releases were used to compare travel times, arrival distributions, and relative recovery efficiencies in the bypass system at Rocky Reach Dam. For the comparative study, only the radio- and PIT-tagged fish detected downstream at Rocky Reach Dam within the bypass system were analyzed to ensure comparable travel distances.

Steelhead smolts used in this investigation were run-of-river fish collected in the juvenile bypass system at Rocky Reach Dam. Smolts were transported to remote tagging–holding stations situated at each of the three dams (i.e., Wells, Rocky Reach, and Rock Island dams). The fish were transported in tanks on a flatbed truck at a density that did not exceed 1 fish·3.785 L^{-1}. During transport, the fish were supplied supplemental oxygen from compressed air tanks housed on the trucks.

To assess whether smolts killed during dam passage might drift downstream and be detected at the subsequent dams, 20 radio-tagged steelhead smolts were killed and released (10 replicate releases of two fish each) concurrent with the other fish releases. These fish were used to assess the probability of false-positive detections of dead radio-tagged smolts and to possibly adjust survival estimates.

At the time of tagging, smolts were placed in a holding tank containing a 100 mg·L^{-1} solution of MS-222 (tricaine methanesulfonate). Once anesthetized, fish were inspected and those with obvious injuries, excessive descaling, adipose fins (e.g., wild smolts, all hatchery steelhead smolts have adipose fins clipped), or less than 150 mm in fork length were excluded. Radio tags were surgically implanted within the peritoneal cavity of the host fish using procedures described in English et al. (1999). Following implantation, individual fish were held in separate compartments (approximately 9.5 L) in a flow-through water delivery system to prevent tangling of the external antennas. The smolts were allowed to recover in ambient river water for 40–48 h before release. Each tagging site had identical fish-holding facilities. Immediately preceding release, each tag was scanned and coded to ensure proper functioning.

Releases at Wells and Rocky Reach tailraces occurred sequentially with the Rocky Reach releases 1 day after the Wells tailrace release. The fish were released at Rock Island tailrace 2 days after the releases at Rocky Reach Dam. The staggered release times were used to help ensure downstream mixing of the smolts so that they might share common downstream survival and detection probabilities. All tag releases occurred at approximately 1600 hours. At each project, the fish were ferried to the release sites, which were mid-channel, approximately 0.5 km downstream of each dam.

Converting radio signals into detection histories

The multitude of radio antennas and associated receivers recorded vast numbers (i.e., approximately 3.1 million records) of radio signals that had to be processed to derive useful and reliable detection histories for survival analysis. These radio signals included multiple hits from alive fish, potentially dead fish, and fish not yet released as well as spurious signals. The role of signal processing was to identify true detections of radio-tagged smolts from

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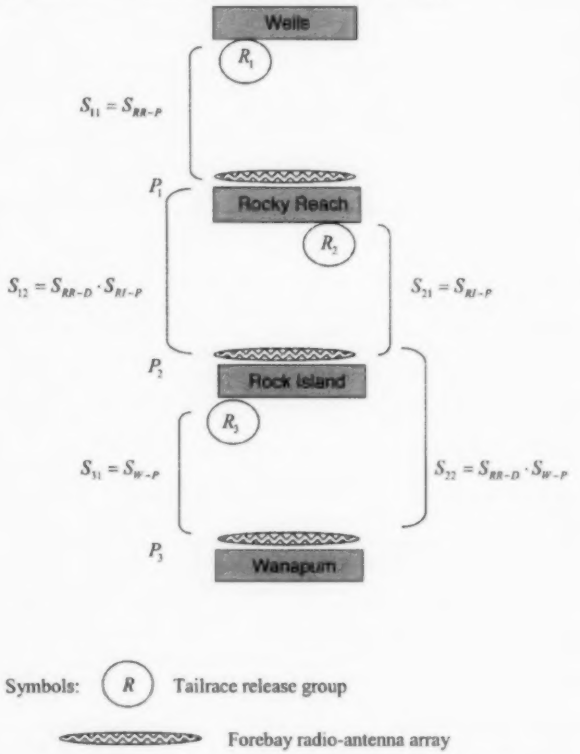
spurious hits. Otherwise, false-positive detections could improperly inflate subsequent survival estimates.

Valid fish targets at a detection site were identified by sorting and filtering the radio-signal data using multiple criteria. The radiotelemetry data were sorted, filtered, and assigned detection histories using alternative criteria for (*i*) the power threshold level of the signal, (*ii*) the frequency of the radio-tag signals per unit of time, and (*iii*) the geographic distribution of the radio signals within the antenna arrays at a site. The power threshold was the minimum power level of a radio signal at a antenna that was considered a valid tag transmission. A distribution of power levels was constructed for each antenna based on signals known not to have come from tagged fish. These signals were collected before releasing the tagged fish or after tagged fish had left the area. These false signals are typically at relatively low power levels. A power threshold was then uniquely established for each antenna to exclude most false signals while recognizing higher power levels as possible valid tag signals. Signal frequency was the minimum number of consecutive signal transmissions above the power threshold required for a detection to be considered valid. Background radio signals not only have typically lower power levels but also occur erratically and irregularly over time. In contrast, the radio tags are preprogrammed to send radio signals at regular intervals. A frequency criterion was used to help distinguish between the frequent signals likely to have come from radio tags from the sporadic signals from background sources. Again, the analysis of signals from background sources was used to establish signal frequency thresholds. Two signal frequencies were considered, 2 or 3 detections/15 min. The third criterion was the geography and the number of antennas that were treated as a single unit in processing the radiotelemetry data and assessing the signal frequency. The antenna arrays at the hydroprojects cover large geographic areas. It is not uncommon for two or more antennas to receive signals from the same tagged fish. However, the detections over time and locations must be consistent with possible movements of the smolt. Signals from disparate locations received over time intervals too short to be realistic smolt movements may suggest signals from background sources. Consequently, antenna arrays were grouped into geographic zones to examine the spatial integrity of the received signals. A "coarse-grained" configuration grouped all antennas at a powerhouse together and separately grouped all spillway antennas together. A second "fine-grained" configuration treated the primary aerial and secondary underwater antenna arrays at the powerhouses and spillways separately.

The construction of detection histories for the radio-tagged steelhead smolts was based on cross-validation using multiple reanalyses of the raw radiotelemetry data. Three alternative sets of processing criteria were used to initially process the radiotelemetry data: (*a*) coarse-grained geography and a frequency threshold of 2 detections/15 min, (*b*) coarse-grained geography and a frequency threshold of 3 detections/15 min, and (*c*) fine-grained geography and a frequency threshold of 2 detections/15 min.

Smolts identified by each of the multiple sets of processing criteria were considered to be valid detections and were included in the detection histories. Radio codes for smolts registered as valid by one but not all data processing criteria were reexamined manually to determine their detection histories. This manual inspection reexamined all radio-signal records of a tag code to determine whether the spatial and temporal patterns of detection, along with power levels, were consistent with the presence of a valid tag code. Although the automated processing of the data can identify classes of data patterns that are programmed, visual inspection can identify patterns or inconsistencies not programmed for inspection. If the manual inspection could not clearly ascertain the validity of a radio-signal record, the detection history of the smolt was right-censored (Elandt-Johnson and Johnson 1980; Lee 1992) to the last location where it was known to be alive. By using multiple processing criteria, an internal quality control procedure was established to help assure that all designated detections at a site were indeed valid radio-tag signals. As a final step in the signal processing, the radiotelemetry data were independently reviewed by staff at LGL Limited of Sidney, B.C., Canada, to provide an outside peer review of the signal processing results.

Fig. 2. Schematic of radio-tag release design and associated survival (*S*) and detection (*P*) probabilities in the 1999 mid-Columbia River radiotelemetry smolt survival study.



An essential element of the signal processing was to analyze the radiotelemetry data independently at each of the three dams. This independent analysis was essential to assure statistical independence of the upstream and downstream detection histories and provide valid survival estimates. To further assess the possibility of including false-positive detections in the capture histories, a sensitivity analysis was performed to assess the effect of alternate signal processing criteria on the resulting survival estimates.

Statistical methods

Parameter estimation

To help ensure all radiotelemetry detections were of alive-tagged fish, detection arrays were placed on the upstream sides of the dams (Fig. 2). Survival probabilities were consequently estimated between the initial release sites and subsequent downstream radio-antenna arrays (Fig. 2). For instance, the Wells Dam tailrace release (i.e., R_1, Fig. 2) was capable of providing information on survival in Rocky Reach pool, followed by the combined Rocky Reach Dam and Rock Island pool survival probability, etc. Hence, unlike the PIT-tag methods of Skalski et al. (1998), survival estimates of direct inference from radio-tag studies included pool survival or survival through the dam of one project and the pool (i.e., reservoir) of the next project. Therefore, concurrent releases of tagged smolts from two sites were necessary in this study to sepa-

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rately estimate the components of the dam and pool survival and reconstruct project survival mathematically (i.e., $S_{\text{Project}} = S_{\text{Pool}} \cdot S_{\text{Dam}}$).

The survival estimation was based on a joint likelihood function that describes the detection histories for each release group (i.e., R_1, R_2, and R_3, Fig. 2) through a maximum of two downstream projects. Fish were radio-tracked for a maximum of only two projects to minimize possible effects of battery failure and the chronic stress of tagging. The first release group (R_1) at Wells Dam tailrace (Fig. 2) had a likelihood function described as follows:

$$(1)\quad L(S_{11},S_{12},P_{11},P_{12} \mid R_1, \underline{x}) \propto (S_{11}P_{11}S_{12}P_{12})^{x_{11}} \times (S_{11}(1-P_{11})S_{12}P_{12})^{x_{01}} \times (S_{11}P_{11}(1-S_{12}P_{12}))^{x_{10}} \times ((1-S_{11}) + S_{11}(1-P_{11})(1-P_{12}S_{12}))^{x_{00}}$$

where x_{ij} is the number of smolts with detection history ij ($i = 0,1$; $j = 0,1$) for detected (1) and nondetected (0) smolts at Rocky Reach (i) and Rock Island (j) dams for release group R_1. The survival parameter S_{12} is the survival probability between Wells tailrace and Rock Reach forebay for release R_1. The survival parameter S_{12} is the survival probability between Rocky Reach forebay and Rock Island forebay for release R_1. The detection parameter P_{11} is the probability that smolts from the R_1 release are detected in Rocky Reach forebay. The detection parameter P_{12} is the probability that smolts from the R_1 release are detected in Rock Island forebay.

For the tailrace release at Rocky Reach Dam (R_2), the likelihood function can be written as

$$(2)\quad L(S_{21}, S_{22}, P_{21}, P_{22} \mid R_2, \underline{y}) \propto (S_{21}P_{22}S_{22}P_{23})^{y_{11}} \times (S_{21}(1-P_{22})S_{22}P_{23})^{y_{01}} \times (S_{21}P_{22}(1-S_{22}P_{23}))^{y_{10}} \times ((1-S_{21}) + S_{21}(1-P_{22})(1-S_{22}P_{23}))^{y_{00}}$$

where y_{ij} is the number of smolts with detection history ij ($i = 0,1$; $j = 0,1$) for detected (1) and nondetected (0) smolts at Rock Island (i) and Wanapum (j) dams for release group R_2. The survival parameter S_{21} is the survival probability between Rocky Reach tailrace and Rocky Island forebay for release R_2. The survival parameter S_{22} is the survival probability between Rock Island forebay and Wanapum forebay for release R_2. The detection parameter P_{22} is the probability that smolts from the R_2 release are detected in Rock Island forebay. The detection parameter P_{23} is the probability that smolts from the R_2 release are detected in Wanapum forebay.

For the tailrace release at Rock Island Dam (R_3), the likelihood function can be written as

$$(3)\quad L(S_{31}, P_{33} \mid R_3, z) \propto (S_{31}P_{33})^{z}(1-S_{31}P_{33})^{R_3-z}$$

where z is the number of smolt detected at Wanapum forebay from release R_3. The survival parameter S_{31} is the survival probability between Rock Island tailrace and Wanapum forebay for release R_3. The detection parameter P_{33} is the probability that smolts from the R_3 release group are detected in Wanapum forebay.

As so far developed, the joint likelihood model for the detections $\underline{x}$, $\underline{y}$, and z is overparameterized, and model parameters cannot be estimated. However, if downstream mixing occurs and the release groups share common downstream survival and capture processes, then the number of model parameters can be reduced and reparameterized where $S_{11} = S_{RR-P}$ is the Rocky Reach pool survival, $S_{12} = S_{RR-D} \cdot S_{RI-P}$ is the Rocky Reach dam survival × Rock Island pool survival, $S_{21} = S_{RI-P}$ is the Rock Island pool survival, $S_{22} = S_{RI-D} \cdot S_{W-P}$ is the Rock Island Dam survival × Wanapum pool survival, and $S_{31} = S_{W-P}$ is the Wanapum pool survival. The detection parameters can also be re-expressed as $P_{11} = P_1$, $P_{12} = P_{22} = P_2$, and $P_{23} = P_{33} = P_3$ when downstream mixing has occurred. It must be also noted that the survival process in the last reach from Rock Island tailrace to Wanapum forebay and the detection at Wanapum Dam are not separable such that $S_{W-P} \cdot P_3 = \lambda$. The joint likelihood for the release–recapture study can thus be written as a product of likelihoods 1–3 where

$$(4)\quad L(S_{RR-P}, S_{RR-D}, S_{RI-P}, S_{RI-D}, P_1, P_2, \lambda \mid \underline{x}, \underline{y}, z) \propto (S_{RR-P}P_1S_{RR-D}S_{RI-P}P_2)^{x_{11}}(S_{RR-P}(1-P_1)S_{RR-D}S_{RI-P}P_2)^{x_{01}} \times (S_{RR-P}P_1(1-S_{RR-D}S_{RI-P}P_2))^{x_{10}} \times (1-S_{RR-P}+S_{RR-P}(1-P_1)(1-S_{RR-D}S_{RI-P}P_2))^{x_{00}} \times (S_{RI-P}P_2S_{RI-D}\lambda)^{y_{11}}(S_{RI-P}(1-P_2)S_{RI-D}\lambda)^{y_{01}} \times (S_{RI-P}P_2(1-S_{RI-D}\lambda))^{y_{10}} \times (1-S_{RI-P}+S_{RI-P}(1-P_2)(1-S_{RI-D}\lambda))^{y_{00}} \times \lambda^{z}(1-\lambda)^{R_3-z}$$

Likelihood 4 has seven parameters and seven minimum sufficient statistics, making estimation possible. The maximum likelihood estimates (MLE) were solved numerically using Program FLETCH (Fletcher 1970), and the standard errors for the parameters were calculated based on the inverse Hessian matrix. Survival rates through the pools and dams were estimated directly from the joint likelihood (eq. 4). Total project survivals were estimated by the product

$$(5)\quad \hat{S}_{\text{project}} = \hat{S}_P \cdot \hat{S}_D$$

with approximate variance estimator

$$(6)\quad \widehat{\text{Var}}\,(\hat{S}_{\text{project}}) = \hat{S}^2_{\text{project}}\left[\widehat{\text{CV}}^2(\hat{S}_P) + \widehat{\text{CV}}^2(\hat{S}_D) + \frac{2\,\widehat{\text{Cov}}(\hat{S}_P, \hat{S}_D)}{\hat{S}_P, \hat{S}_D}\right]$$

where CV refers to the coefficient of variation. Profile likelihood confidence intervals at $(1-\alpha)\,100\% = 95\%$ were calculated for the survival parameters (Hudson 1971).

Model assumptions

Release groups R_1 and R_2 provide data to estimate reach survival based on the single release–recapture model (Skalski et al.1998). There are seven assumptions associated with the single release–recapture model. The key assumptions of the single-release model are described here.

(A1) Individuals marked for the study are a representative sample from the population of interest.

(A2) Survival and capture probabilities are not affected by tagging or sampling, that is, tagged animals have the same survival probabilities as untagged animals.

(A3) All sampling events are "instantaneous", that is, sampling occurs over a negligible distance relative to the length of the intervals between sampling events.

(A4) The fate of each tagged individual is independent of the fate of all others.

(A5) All tagged individuals alive at a sampling location have the same probability of downstream survival.

(A6) All tagged individuals alive at a sampling location have the same probability of being detected.

(A7) All tags are correctly identified and the status of smolt (i.e., alive or dead) is correctly assessed.

The first assumption (A1) concerns making inferences from the sample to the target population. For example, if inferences are sought for wild steelhead smolts, then the sample of tagged fish should be drawn from that class of fish. Otherwise, nonstatistical inferences are necessary, justifying the similarity between the target population and the representativeness of radio-tagged fish. This

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assumption could also be violated if smolts selected for radio tagging were on the average larger than the population of smolts in general. In this study, inference is to run-of-river steelhead smolts ≥150 mm in length.

Assumption A2 again relates to making inferences to the population of interest (i.e., untagged fish). If tagging has a detrimental effect on survival, then the survival probabilities derived from radio-tagging experiments will tend to be underestimated. In the paired-release study performed, tagging might be expected to affect upstream and downstream release groups similarly, and thereby, the bias might be minimized or eliminated when the ratio of survivals is calculated.

The third assumption (A3) specifies that mortality is negligible immediately in the vicinity of the sampling stations, so that the estimated mortality is related to the river reaches in question and not during the sampling event. In the case of outmigrating smolts, the time spent in the vicinity of an antenna array is brief and the area small, relative to the size of the river reaches in question. This assumption should be fulfilled by the speed of the outmigration through the antenna arrays.

The assumption of independence (A4) implies that the survival or death of one smolt has no effect on the fates of the others. In a large river system with tens or hundreds of thousands of smolts, this is likely true. Furthermore, this assumption is common to all tag analyses with little or no evidence collected to suggest it is not generally true. Even so, violations of assumption A4 have little effect on the point estimate but might negatively bias the variance estimate because the effective sample size would be smaller than perceived.

Assumption A5 specifies that the prior detection history of a smolt has no effect on subsequent survival. The lack of handling following initial release of radio-tagged smolts in radiotelemetry studies minimizes the risk that subsequent detections influence survival. Similarly, assumption A6 could be violated if downstream detections were influenced by upstream passage routes taken by the smolts. Violation of this assumption was minimized in this study by placing antenna arrays across the breadth of the river.

Assumption A7 implies that smolts do not lose their tags to be subsequently misidentified as dead or not detected, and dead fish are not falsely recorded as alive at detection locations. The use of surgically implanted tags should have minimized the chance of tag loss. Tag loss and radio failure would tend to result in a negative bias (i.e., underestimation) of smolt survival rates. The possibility of radio failure will depend on travel time relative to battery life. To minimize the chance of radio failure in this study, smolts were tracked for only two reaches below their release location. Dead fish drifting downstream could result in false-positive detections and upwardly bias survival estimates. Tailrace antenna arrays were not used in this study for this reason. This assumption could also be violated if the radiotelemetry data were misinterpreted. To minimize the chances of misinterpretation, the radiotelemetry data were independently interpreted by staff at the University of Washington and LGL Limited and cross-validated. In addition, sensitivity analyses were performed to assess the effect of choices of signal processing criteria on subsequent survival estimates.

To estimate survival components from the paired releases, for example,

$$(7)\qquad E\left[\frac{\hat{S}_{12}}{\hat{S}_{21}}\right] \doteq \frac{S_{RR-D}\cdot S_{RI-P}}{S_{RI-P}} = S_{RR-D}$$

two additional assumptions for valid survival estimation are necessary. (A8) Survival in the lower river segments is conditionally independent of survival in the upper river segments. In other words, releases (R_1) and (R_2) experience the same survival probability in the lower river segment (S_{RI-P}), and similarly, (A9) releases (R_2) and (R_3) experience the same survival probability in the lower river segment (S_{W-P}). Assumption A8 implies that there is no synergistic relationship between survival processes in the different river segments. In other words, smolts that survive the first river segment are no more or less susceptible to mortality in the second river segment than smolts released in the second river segment.

Inspection of eq. 7 also indicates that if delayed mortality associated with dam passage exists or vitality is reduced by repeated hydroproject passage, then survival in the common pool may not be equal for both upstream and downstream releases, i.e.,

$$(8)\qquad E\left[\frac{\hat{S}_{12}}{\hat{S}_{21}}\right] \doteq \frac{S_{RR-D}\cdot S'_{RI-P}}{S_{RI-P}} \neq S_{RR-D}$$

thereby biasing the survival estimates accordingly. In studies with multiple downstream (i.e., minimum of 3) detection sites per release group, Burnham et al. (1987) tests 2 and 3 can be used to assess whether upstream detection histories have an effect on downstream detection and survival. However, the battery life of the radio tags limits how long and how far downstream smolts can be monitored, precluding such tests as in the case of this study.

One advantage of the ratio estimates used in this analysis is that estimates of project survival should be rather robust to post-release handling mortality. For example, Rocky Reach project survival would be expressed as

$$S_{RR} = \frac{S_{11}\cdot S_{12}}{S_{21}}$$

In the case of post-release handling mortality (i.e., $1 - S_H$) that acts equally on all release groups, the estimate of Rocky Reach project survival is unchanged where

$$(9)\qquad \frac{(S_{11}\cdot S_H)S_{12}}{(S_{21}\cdot S_H)} = \frac{S_{11}\cdot S_{12}}{S_{21}} = S_{RR}$$

The same relationship will hold true for Rock Island project survival estimates. Assumption A9 can be satisfied by the downstream mixing of the two release groups (i.e., R_1 and R_2, R_2 and R_3) but it can also be satisfied if the survival process is stable over the course of smolt passage.

Tests of assumptions

The assumption of downstream mixing among the releases of smolts (e.g., R_1 and R_2, R_2 and R_3) was tested using an $R \times C$ contingency table based on the numbers of smolts detected by date and release group. Counts were tallied daily and, when insufficient, pooled across days to ensure proper test performance (Snedecor and Cochran 1967). Alternatively, a two-sample Kolmogorov–Smirnov test of equal distributions could be used to compare arrival patterns (Conover 1980). However, the very strong diel passage of smolts at the hydroprojects makes daily observations a natural unit of observation and the contingency table tests can be readily partitioned to assess where differences in arrival may exist. The releases of 20 dead radio-tagged smolts from each tailrace were used to estimate false-positive rates of detection of tagged but dead smolts to potentially adjust reach survival for bias.

Comparison of PIT-tagged and radio-tagged smolt behavior

Three interrelated analyses were performed to compare the outmigration dynamics of PIT-tagged and radio-tagged steelhead smolts. For each tag type, mean travel time was computed using the harmonic mean ($\bar{t}_H$)

$$(10)\qquad \bar{t}_H = \frac{n}{\sum_{i=1}^{n}\frac{1}{t_i}}$$

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with approximate variance estimator

$$(11)\quad \widehat{\mathrm{Var}}\ (\bar{t}_H) = \frac{S^2_{1/t}}{n\hat{\mu}^4_{1/t}}$$

where t_i is the travel time from Wells to Rocky Reach Dam for the ith smolt detected ($i = 1,\ldots, n$) at Rocky Reach Dam bypass. Calculation of the variance estimate for a harmonic mean includes the following intermediate calculations:

$$(12)\quad S^2_{1/t} = \frac{\sum_{i=1}^{n}\left(\frac{1}{t_i} - \hat{\mu}_{1/t}\right)^2}{(n-1)}$$

and

$$(13)\quad \hat{\mu}_{1/t} = \frac{1}{n}\sum_{i=1}^{n}\frac{1}{t_i}$$

The harmonic mean was an appropriate measure of the central tendency when analyzing travel speed (Freund 1988). An asymptotic Z test was used to compare harmonic means at $\alpha = 0.10$.

Arrival distributions to Rocky Reach Dam were compared using an $R \times C$ contingency table test of homogeneity based on the dates of arrival for each tag type. The proportions of PIT-tagged and radio-tagged steelhead detected in the Rocky Reach bypass system were compared using a 2×2 contingency table test of homogeneity. All tests were performed at $\alpha = 0.10$.

Sensitivity analyses

Sensitivity analyses were performed to assess how much the estimates of project survival were influenced by the criteria used in processing the raw radiotelemetry data. The use of too liberal of inclusion criteria in the signal processing will falsely inflate the survival estimates. As the processing criteria used to designate a radio signal as a valid tag signal becomes more rigorous, the detection probabilities at the dam sites will decrease, but the survival estimates should be relatively stable with the standard errors of the estimates increasing as the detection rates decrease. Two types of sensitivity analyses were performed. The first examined the effect of changing the signal frequency criterion. The number of consecutive signal detections within a geographic zone used to designate a valid tag detection was varied from 1 to 60 per 15 min. Antenna power thresholds were held at their optimal settings during this first set of sensitivity analyses. In the second set of analyses, the power thresholds at all antennas were uniformly varied over a range of 10 to 70. During these sensitivity analyses, the frequency criterion was held at the nominal level of 3 signals per 15 min.

Results

Survival estimation

A total of 249, 251, and 250 radio-tagged steelhead smolts were released from Wells, Rocky Reach, and Rock Island tailraces, respectively. Detection histories of the steelhead smolts among the various release groups are summarized in Table 2. Plots of the arrival distributions of releases R_1 and R_2 at Rock Island Dam and R_2 and R_3 at Wanapum Dam suggest reasonably good mixing of upstream and downstream releases (Fig. 3). However, the χ^2 tests of homogeneity for R_1 and R_2 ($(\chi^2_{14} \geq 28.2333) = 0.01$) and R_2 and R_3 ($(\chi^2_{15} \geq 26.3470) = 0.03$) were significant. The arrival distributions show similar modes but perhaps a 1-day offset between releases R_1 and R_2 at Rock Island Dam. The arrival distributions for releases R_2 and R_3 at Wanapum Dam showed similar timing of the modes but somewhat different amplitudes. Similar flow and dam operations during the days of passage suggest similar detection and survival probabilities were likely.

Table 2. Summary of counts of steelhead smolts by detection history for each release group.

	Detection histories at Rocky Reach and Rock Island Dams				
Release	11	01	10	00	Total
R_1	192	14	26	17	249
	Detection histories at Rock Island and Wanapum Dams				
	11	01	10	00	Total
R_2	173	24	42	12	251
	Detection histories at Wanapum Dam				
	1	0			Total
R_3	197	53			250

Note: 1 denotes detection; 0 denotes nondetection at a downstream site.

The dead radio-tagged smolts released in the tailraces of Wells, Rock Island, and Rocky Reach dams suggested no potential problem of false-positive detections associated with the mortality of smolts during upstream passage at the hydroprojects. No smolts known to be dead were detected downstream of their release locations. These results, in combination with the similar arrival distributions of the release groups, suggest that survival estimates using the radiotelemetry method were appropriate in this study.

Pooling the detection histories from the releases over time, the joint likelihood (eq. 4) was used to estimate survival and detection probabilities at Rocky Reach and Rock Island dams (Table 3). Maximum likelihood estimation produced separate pool and dam survival estimates at Rocky Reach of $\hat{S}_{RR-P} = 0.9393$ (95% confidence interval (CI), $(0.9030 < S_{RR-P} < 0.9671) = 0.95$) and $\hat{S}_{RR-D} = 1.0282$ (CI, $(0.9572 < S_{RR-D} < 1.0) = 0.95$), respectively. Combining the pool and dam results, total project survival at Rocky Reach was estimated to be $\hat{S}_{RR} = 0.9658$ (CI, $(0.9050 < S_{RR} < 1.0) = 0.95$). For Rock Island, pool and dam survival probabilities were estimated to be $\hat{S}_{RI-P} = 0.9751$ (CI, $(0.9421 < S_{RI-P} < 0.9812) = 0.95$) and $\hat{S}_{RI-D} = 1.0238$ (CI, $(0.9527 < S_{RI-D} < 1.0) = 0.95$], respectively. For Rock Island, the subsequent project survival for steelhead smolts was estimated to be $\hat{S}_{RI} = 0.9983$ (CI, $(0.9284 < S_{RI} < 1.0) = 0.95$).

Sensitivity analyses

The project survival estimates at Rocky Reach varied from 0.95 to 1.10 as the criterion for the number of radio signals/15 min (i.e., signal frequency) used in obtaining detection histories was varied (Fig. 4). The estimate of Rocky Reach project survival calculated from using the signal processing criteria used in the formal analysis presented earlier was $\hat{S}_{RR} = 0.9658$ (CI, $(0.9050 < S_{RR} < 1.0) = 0.95$). As expected, the detection probabilities decreased monotonically as the frequency requirement increased (Fig. 4). For Rock Island, project survival estimates varied from 0.94 to 1.01 over the same range of frequency criterion (the best estimate was considered to be $\hat{S}_{RI} = 0.9983$).

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Fig. 3. Plots of the arrival distributions at downstream dams for the paired releases used in the radiotelemetry model (eq. 4) for (*a*) releases R_1 and R_2 detected at Rock Island Dam and (*b*) releases R_2 and R_3 detected at Wanapum Dam. Arrival distributions for the Wells tailrace release (R_1) are denoted by ◆, Rock Island tailrace release (R_2) are denoted by □, and the Rock Island tailrace releases are denoted by ▲.

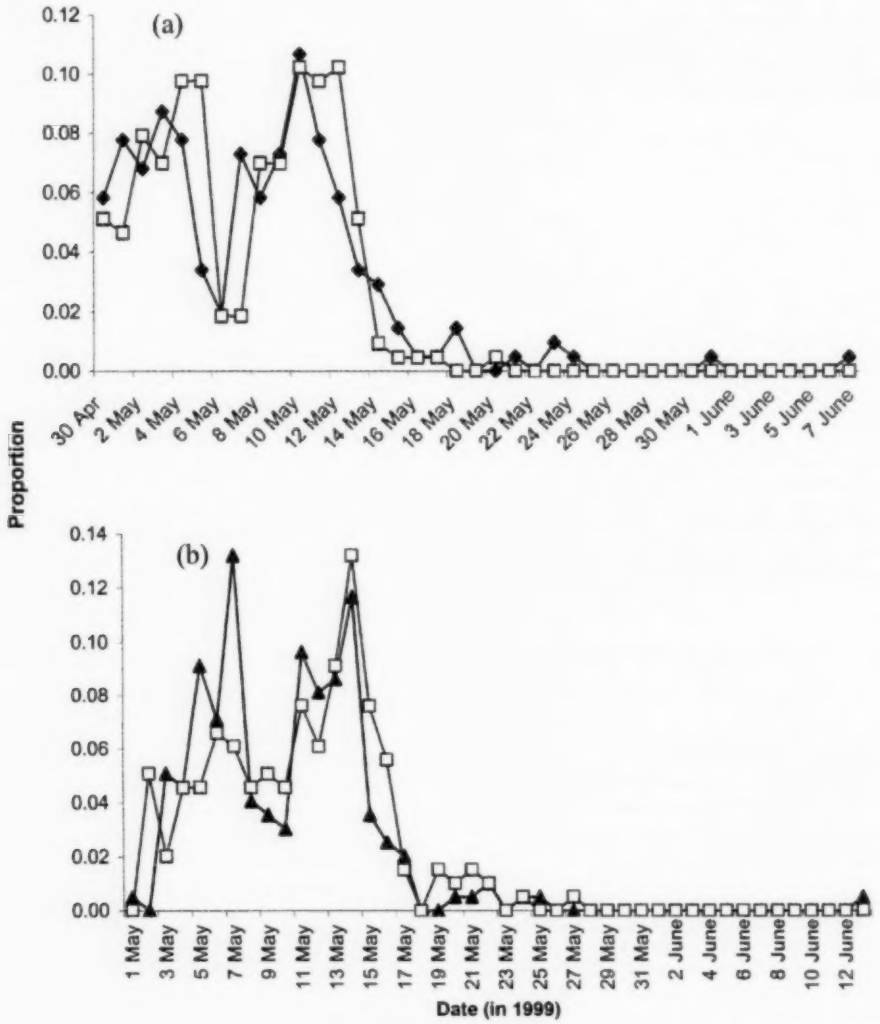

Table 3. Summary of survival parameters estimated from the 1999 radiotelemetry study (standard errors are in parentheses).

	Project	
Parameter	Rocky Reach	Rock Island
Pool (S_{Pool})	0.9393 (0.0163)	0.9751 (0.0150)
Dam (S_{Dam})	1.0282 (0.0369)	1.0238 (0.0484)
Project ($S_{Project}$)	0.9658 (0.0375)	0.9983 (0.0467)
Detection probability (P)	0.9320 (0.0175)	0.8785 (0.0233)
Joint survival and detection at Wanapum Dam	0.7880 (0.0259)	

Changing the power threshold criterion over the range of 10 to 70 caused the Rocky Reach project survival estimates to vary from approximately 0.96 to 0.99. The Rock Island project survival estimates varied from 0.995 to 1.005 over the same power threshold range. In general, the sensitivity analyses support the reported project survival estimates. Average survival estimates generated from the sensitivity analyses were close to reported values (Fig. 4). This study and experience analyzing other radio-tag studies elsewhere (English et al. 2000; Miller et al. 2000; Skalski et al. 2001) suggest that the power threshold criterion is less influential than the frequency criterion on subsequent survival estimates.

During the course of this radio-tag investigation, over 3.1 million radio signals were received and processed. Hence, computer analysis is essential when interpreting vast amounts of signal data. Nevertheless, careful manual inspection of the data is still required. When alternative computer processing criteria did not agree with the designation of a valid target, manual inspection was used. Information on the

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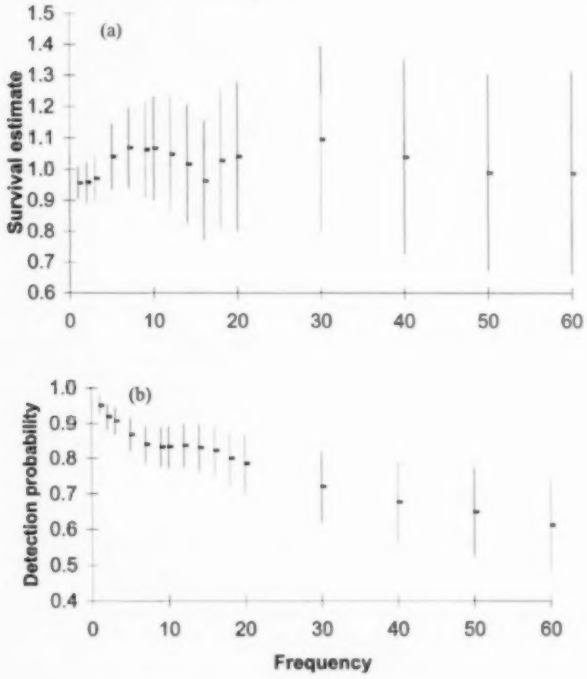
Fig. 4. Plots of (*a*) Rocky Reach project survival estimates and (*b*) detection probabilities versus the number of detections/15 min used to designate a valid signal in a series of sensitivity analyses. CIs of 95% are reported.



power levels and the spatial and temporal sequence of the received signals were used to assess the logical consistency of the data and whether a valid target existed or not. If this failed, the detection histories were right-censored at the last location where the smolts were known to be alive. Hence, a multistage, multicriteria processing scheme, as performed in this study, should be more reliable than the uninformed use of blanket criteria as applied in this sensitivity analysis.

Comparison of radio-tagged and PIT-tagged smolt outmigration behavior

For the PIT-tagged steelhead, harmonic mean travel time was estimated to be $\bar{t}_H = 1.659$ days ($n = 259$, $\widehat{SE} = 0.042$) from Wells tailrace to Rocky Reach Dam. For radio-tagged steelhead, the travel time was estimated to be $\bar{t}_H = 1.875$ days ($n = 136$, $\widehat{SE} = 0.074$). Their very similar travel times were, however, significantly different ($P(|Z| > 2.54) = 0.01$). Practically speaking, these mean travel times were likely not different enough to be considered biologically meaningful (i.e., 5.2 h). In performing this analysis, only the radio-tagged smolts that were detected within the bypass system were used in the calculation of travel time. In this way, both the PIT- and radio-tagged smolts have the same terminus.

The arrival distributions of the PIT-tagged and radio-tagged steelhead at the Rocky Reach bypass were nearly identical (Fig. 5). Nevertheless, a very sensitive χ^2 test of homogeneity found the arrival distributions to be different ($P(\chi^2_6 > 14.7137) = 0.02$). In performing the analysis, counts for days 7 and beyond were pooled. More detailed inspection found that the arrival distributions were homogeneous for the first 6 days after release ($P(\chi^2_5 > 4.0468) = 0.54$). However, the arrival distributions differed in the higher proportion of radio-tagged smolts that took 7 or more days to make the journey. This is consistent with the slightly long harmonic mean travel time of radio-tagged steelhead smolts.

The observed proportions of PIT-tagged ($p = 0.51$, $n = 508$) and radio-tagged ($p = 0.55$, $n = 249$) steelhead smolts that survived to Rocky Reach Dam and were diverted and detected in the bypass systems were not significantly different ($P(\chi^2_1 > 0.7488) = 0.39$). This test suggests that the survival and collection probabilities of PIT- and radio-tagged steelhead smolts were similar over the 68-km reach examined.

Discussion

The travel speed, survival, and the bypass diversion probabilities of radio-tagged steelhead were very similar to the less invasively PIT-tagged steelhead smolts. These results suggest survival estimates from radiotelemetry studies may be as reliable as those obtained from less intrusive PIT-tagging procedures.

Empirical results from the radio-tag study also suggest reasonable mixing of upstream and downstream releases may have been achieved. However, χ^2 tests of mixing were significant. Great care must be taken in performing a proper paired-release design. The prospects of mixing tend to decrease as the distance between upstream and downstream releases increases. Historically, paired releases over one or more river reaches have had difficulty in achieving complete mixing (Bickford and Skalski 2000).

One advantage of the paired-release design, however, over the single-release model used with PIT-tag studies to estimate smolt survival (Skalski et al. 1998) is the potential ability to reduce bias associated with delayed tagging or handling effects. If post-release handling effects existed, then the effects would be expected to be similar for upstream and downstream releases and the effect would be canceled in the ratio estimate, providing an unbiased estimate of project survival (eq. 9). On other hand, pool survival is estimated directly from likelihood (eq. 4) and any post-release handling mortality would bias the estimate downward. Dam survival would conversely be estimated with a positive bias. This is what may have occurred during the investigation. The out-of-range estimates of dam survival of 1.0282 and 1.0238 at Rocky Reach and Rock Island dams, respectively, may be an indication of such consequences. Longer holding times to allow delayed handling effect to dissipate under more realistic river environments may help eliminate any delayed mortality and improve subsequent survival estimates.

Muir et al. (1995) also found that partitioning project survival into dam and pool components using PIT-tag releases problematic. In that study, forebay and tailrace paired releases of PIT-tagged smolts were used to estimate dam survival. The forebay releases can result in unrealistic passage distributions at the dam that do not mimic the natural migration pattern and subsequently biased the dam survival estimates. An advantage of the radiotelemetry technology is that the problematic forebay releases are not needed to estimate dam survival.

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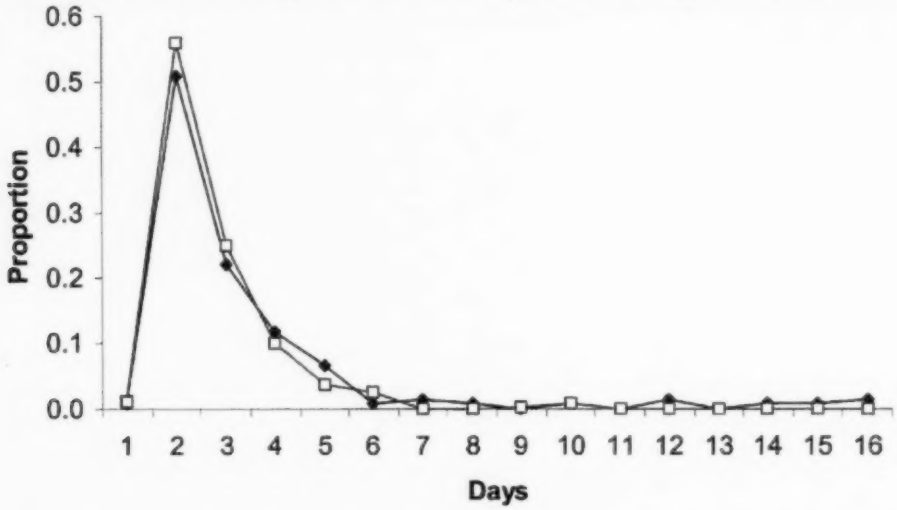
Fig. 5. Plots of travel time distributions for PIT- and radio-tagged steelhead smolts from Wells Dam tailrace to Rocky Reach Dam PIT-tag detector. Arrival distributions for the radio-tagged smolts are denoted by ◆ and the PIT-tagged smolts are denoted by □.



This study estimated the survival probability of 0.9658 ($\widehat{SE}$ = 0.0375) at Rocky Reach and 0.9983 ($\widehat{SE}$ = 0.0467) at Rock Island. Concurrent PIT-tag survival studies at the Rock Island project using hatchery steelhead estimated a mean survival of 0.958 ($\widehat{SE}$ = 0.014) based on 20 replicate paired-release studies (Stevenson et al. 2000). These PIT-tag and radio-tag survival estimates are not significantly different (P = 0.41). In a PIT-tag study performed by Douglas County Public Utility District, smolt passage through the Rocky Reach project was estimated to have a mean survival probability of 0.959 ($\widehat{SE}$ = 0.010) for hatchery steelhead from 15 replicate single-release studies in 1999 (Bickford et al. 2000). Again, these PIT-tag and radio-tag survival estimates at Rocky Reach are not significantly different (P = 0.86).

Increasingly, attention is shifting from simply deriving project survival estimates to estimates of pool, dam, or even route-specific survival. This detailed information is needed to monitor and evaluate expensive mitigation projects at the hydroprojects and to focus new mitigation effects for maximum benefit. Radiotelemetry methods hold the promise of providing this detailed information with fewer test fish at a time when massive fish tagging studies using more conventional methods are no longer feasible because of ESA listings of salmonid stocks. The radiotelemetry methods presented in this paper thus provide an additional investigative tool in the battle to preserve and recover endangered salmonid resources in the Columbia River Basin.

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Response of fish communities to different levels of white sucker (*Catostomus commersoni*) biomanipulation in five temperate lakes

Philippe Brodeur, Pierre Magnan, and Michel Legault

Abstract: The goal of this study was to evaluate the response of white sucker (*Catostomus commersoni*), brook trout (*Salvelinus fontinalis*), and other fish species to the mass removal of white sucker in five Québec (Canada) lakes. White sucker removal ranged from 14.2 kg·ha^{-1} to 31.3 kg·ha^{-1} 3 years after mass removal. In four of the study lakes, the proportion of 2+ to 4+ white sucker increased following mass removal. Mean catch and biomass per unit of effort of 1+ brook trout increased significantly in the lakes where white sucker removal was highest. All white sucker populations experienced growth increases after mass removal, and improved brook trout growth was observed in lakes where the most intensive mass removal occurred. These growth increases led to higher mean length at maturity in white sucker females and decreases in mean age at maturity in white sucker males and brook trout males and females. Mean adjusted fecundity significantly increased in white sucker and brook trout in lakes where mass removal was most intense. The present study suggests that white sucker and brook trout exhibit compensatory responses following a reduction of intra- and inter-specific competition and that these responses are related to the intensity of mass removal.

Résumé : Le but de cette étude était d'évaluer la réponse du meunier noir (*Catostomus commersoni*), de l'omble de fontaine (*Salvelinus fontinalis*) et des autres espèces présentes face au retrait massif du meunier noir dans cinq lacs du Québec (Canada). Le retrait massif du meunier noir a varié entre 14.2 kg·ha^{-1} et 31.3 kg·ha^{-1} après trois ans de retrait massif. La proportion des meuniers de deux à quatre ans (2+ à 4+) a augmenté suite au retrait massif dans quatre des cinq lacs à l'étude. Les prises et biomasses par unité d'effort des ombles de fontaine de un an (1+) ont augmenté significativement dans les lacs où le retrait massif du meunier noir a été le plus important. Toutes les populations de meunier noir ont affiché une augmentation de croissance suite au retrait massif alors que des augmentations de croissance ont été observées chez l'omble de fontaine seulement, dans les lacs où le retrait massif a été le plus intense. Ces augmentations de croissance ont entraîné une augmentation de la longueur à maturité du meunier noir ainsi que des diminutions de l'âge à maturité des mâles du meunier noir et des mâles et femelles de l'omble de fontaine. La fécondité moyenne ajustée des meuniers et des ombles a augmenté dans les lacs où le retrait massif a été le plus important. Cette étude suggère que le meunier noir et l'omble de fontaine affichent des réponses compensatoires suite à des réductions de compétition intra- et interspécifique et que ces réponses sont fonction de l'intensité du retrait massif.

Introduction

Because perturbed systems give insight about the regulating mechanisms involved in nature, the biomanipulation concept, originally developed by Shapiro et al. (1982), has been used in a series of field experiments since its conception. Biomanipulation has been used for water quality improvement and management (Jorgensen and de Bernardi 1998), to study trophic interactions in freshwater lakes through fish removal or stocking (Carpenter et al. 1985; Elser et al. 1995), and to better understand intra- or inter-specific interactions and life-history responses in fishes to variations in the level of these interactions (Johnson 1977; Hayes et al. 1992; Persson and Hansson 1999). Fish removals have also been used in management programmes to restore stunted fish populations (Langeland 1986; Donald and Alger 1989; Amundsen et al. 1993). However, few studies have investigated the response of the whole fish community on several lakes simultaneously.

White sucker (*Catostomus commersoni*), creek chub (*Semotilus atromaculatus*), and some other fish species are present in many brook trout (*Salvelinus fontinalis*) lakes of the province of Québec (Canada). These fish were introduced by bait fisherman, colonised the shield following the creation of new migratory path after human activity (Lacasse and Magnan 1994), or naturally overlap in their distributions (Scott and Crossman 1974). Previous studies indicated that brook trout shift their feeding habits from zoobenthos to zooplankton when living in sympatry with these species (Magnan 1988; Tremblay and Magnan 1991; Lacasse and Magnan 1992). These niche shifts were correlated with significant decreases in mean annual brook trout yield (sport fishing) and relative abundance and biomass (Magnan 1988; Lachance and Magnan 1990). Given the impact of introduced species on the brook trout fishery, the Société de la

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Table 1. General characteristics of the study lakes containing sympatric brook trout and white sucker populations.

Lake	Surface area (ha)	Mean depth (m)	Conductivity ($\mu S \cdot cm^{-1}$)	Secchi depth (m)	Other fish species						
					MM	CP	PE	SA	GA	NC	Others
Mastigou	177	7.0	24	3.1	×		×				
Claudette	110	4.1	15	4.0							
Rimouski	114	4.4	82	2.0	×	×	×	×	×		
Des Iles	347	12.0	19	7.0	×					×	
Cinq Doigts	615	8.9	24	3.0	×	×		×			×

Note: Fish species abbreviations: MM, pearl dace (*Margariscus margarita*); CP, lake chub (*Couesius plumbeus*); PE, northern redbelly dace (*Phoxinus eos*); SA, creek chub (*Semotilus atromaculatus*); GA, threespine stickleback (*Gasterosteus aculeatus*); NC, golden shiner (*Notemigonus crysoleucas*); Others: common shiner (*Luxilus cornutus*), fallfish (*Semotilus corporalis*), longnose dace (*Rhinichthys cataractae*), longnose sucker (*Catostomus catostomus*).

faune et des parcs du Québec (FAPAQ; formerly Ministère de l'Environnement et de la Faune du Québec) initiated an experimental program in 1995 to control white sucker in five Québec brook trout lakes where they had been introduced. This program provides a good opportunity to evaluate the fish community response to a reduction in intra- and inter-specific competition as well as the time required to respond to these changes.

The first objective of the present study was to estimate the white sucker life-history response (relative abundance, age distribution, growth, fecundity, length and age at sexual maturity) after its selective removal. The second objective was to evaluate the response of other fish species (relative abundance for all species; age distribution, growth, fecundity, length and age at sexual maturity in brook trout) following white sucker removal. Fish population structures were compared before, the year of, and 3 years after white sucker mass removal in five experimental lakes.

Materials and methods

Study lakes

The five experimental lakes are located in the province of Québec (Canada): lakes Mastigou, Claudette, Rimouski, des Iles, and Cinq Doigts, situated in Réserve Mastigouche (46°34′N, 73°34′W), ZEC (Zone d'exploitation contrôlée) Martin-Valin (48°40′N, 70°37′W), Réserve Rimouski (48°01′N, 68°12′W), ZEC des Nymphes (46°28′N, 73°35′W), and Réserve Rouge-Matawin (46°36′N, 74°31′W), respectively. These are typical oligotrophic temperate lakes with respect to surface area, mean depth, conductivity, Secchi disk transparency, and thermal stratification (Table 1).

The five study lakes contained sympatric brook trout and white sucker populations. All lakes except Lake Claudette also contained other cyprinid species, but their relative biomass accounted for less than 10% of total fish biomass before mass removal (Table 1). Lake Cinq Doigts also contained longnose sucker (*Catostomus catostomus*) and six cyprinid species that accounted for 45% of total fish biomass (Table 1). Northern redbelly dace (*Phoxinus eos*), threespine stickleback (*Gasterosteus aculeatus*), longnose dace (*Rhinichthys cataractae*), and pearl dace (*Margariscus margarita*), present only in lakes Rimouski and des Iles, were not included in these estimates because they were not caught before mass removal in gillnet samples. The presence of northern redbelly dace did not significantly affect the mean yield of brook trout in other lakes of the same system (P. Magnan, unpublished data), and a funnel-trap sampling in Lake Rimouski revealed that threespine stickleback and pearl dace were captured in low abundances. Our results of mass removal also indicated that the abundance of longnose dace is low in Lake Cinq Doigts. All species that accounted for at least 1% of the total biomass captured during gillnet sampling were considered in the present study. Brook trout populations of all lakes are subject to sport fishing and exploitation is carefully controlled by the Québec government.

White sucker mass removal

Mass removal of adult white suckers was done for 3 consecutive years by the FAPAQ according to an integrated control method proposed by Magnan et al. (1998). White sucker removal started in 1995 for lakes Mastigou, Claudette, and Rimouski and in 1996 for lakes des Iles and Cinq Doigts. Following ice melt and before the maximum water temperature on the spawning grounds reached 10°C, trap nets (mesh size 0.36 cm^2, 1.44 cm^2, or 6.25 cm^2), fyke nets (mesh size 1.56 cm^2), or fishing gear made with fences and retention cages (mesh size 1.25 cm^2, 2.50 cm^2, or 3.13 cm^2) were set near the mouth of streams where white sucker migrate to spawn. Fishing gear were set between April 28 and May 30 and remained operational until June 13 to July 24, depending on lakes and years. All species other than brook trout were removed during mass removal and their total weight was noted.

On some occasions, mature white sucker passed through fishing gear because of water level increases, gear breakage, or both. To prevent any significant recruitment from these individuals, white sucker larvae were controlled up to fishing gear in streams of lakes Mastigou (1995 and 1996), Claudette (1995, 1996, and 1997), des Iles (1996), and Cinq Doigts (1996, 1997, and 1998) by the FAPAQ with 2.5% Nusyn-Noxfish liquid rotenone. The amount of rotenone used depended on stream flow and was calculated to obtain a concentration of 100 ppm for a 1-min contact period (Magnan et al. 1998).

Fish species response to white sucker mass removal

Fish sampling

To evaluate the response of fish species following the reduction of white sucker abundance, experimental gillnet fishing was done before (five lakes), the year of (three lakes), and 3 years after (five lakes) mass removal (Mastigou: 1991, 1995, 1997; Claudette: 1991, 1995, 1997; Rimouski: 1994, 1995, 1997; Cinq Doigts: 1995, 1998; des Iles: 1995, 1998). Gillnetting was done before the brook trout spawning season (between July and September depending on the lake), and in a given lake, it was carried out during the same periods before, the year of (if applicable), and after mass removal. The nets were set randomly, perpendicular to the shore, with small and large meshes alternating from the shore among gillnets (except in Lake Rimouski where small meshes were always set towards the shore). The number of nets used (between 8 and 12) varied among lakes, depending on surface area. Fishing took place for 16–24 h and always covered the period between 1800 and 0900. For lakes Mastigou and Claudette, sampling before and after mass removal was carried out with experimental monofilament gillnets (1.8 m

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deep × 67.5 m long with stretched mesh of 20, 24, 33, 36, 50, 60, 76, 90, and 100 mm and filament diameters of 0.13, 0.15, 0.17, 0.17, 0.17, 0.17, 0.20, 0.20, and 0.25 mm, respectively). In lakes Rimouski, Cinq Doigts, and des Iles, we used experimental multifilament gillnets (1.8 m deep × 38 m long, with stretched mesh of 25, 32, 38, 51, 64, and 76 mm and filament diameter of 0.19, 1.19, 0.26, 0.26, 0.42, and 0.42 mm, respectively) for all sampling periods. These nets were also used for the year of mass removal sampling in lakes Mastigou and Claudette. Each fish captured was identified, weighed (±0.1 g), and measured (±1 mm total length (TL)). Sexual maturity of brook trout was noted and gonads of mature females were preserved in Gilson's fluid (Snyder 1983) for further fecundity estimations (except for the before mass removal sampling in lakes Mastigou, Claudette, and Rimouski). We removed the right pectoral fin of white sucker and scales (from the left side of fish between the dorsal fin and lateral line) of brook trout for age determinations (except for the before mass removal sampling in lakes Mastigou, Claudette, and Rimouski).

To evaluate the impact of white sucker mass removal on its reproductive traits (fecundity and length and age at maturity), we used random samples of 150 individuals distributed in all size classes from those collected during mass removal. Sampling was done during the peak of the spawning migration (late May or early June) of the 1st (1995) and 3rd (1997) year of mass removal in lakes Mastigou, Claudette, and Rimouski. The individuals were processed as above.

Statistical approach

For all response variables described below, we used a mixed-model analysis of variance ANOVA (i.e., general linear model with both fixed and random effects) to test if fish species responded to the white sucker removal (as a treatment). The mixed models included the time period (i.e., before or after) as fixed effect and lake as a random effect. Fish length and age were also used as fixed effects when necessary (fecundity and growth comparisons). It was not possible to include the year as a fixed effect because the effect of year would have been confounded with that of treatment period. We also did a lake-by-lake comparison for each response variable before and after mass removal to understand details particular to each lake and to interpret the results of mixed-model ANOVA (detailed below). As running tests independently on each lake results in a loss of statistical power (thereby weakening the overall conclusions), the lake-by-lake comparisons were used for reference only.

Fish abundance

To evaluate the impact of white sucker removal on species abundance, catch and biomass per unit of effort (CPUE and BPUE, respectively) were estimated from gillnetting. We first tested for the effect of mass removal and lake on CPUE and BPUE of white sucker and brook trout with a mixed model ANOVA. A t test was also used to compare the mean CPUE and BPUE of each species before and after mass removal on each lake (except for lake chub and creek chub in Lake Rimouski, where we compared the year of and 3 years after mass removal). To test for recruitment increase, the same analyses were used to compare the mean relative abundance (CPUE and BPUE) of 2+ white sucker and 1+ brook trout among years for which age data were available. These were the youngest age-classes captured with our gillnets. Also, given the spawning season of each species and the time of mass removal (May to mid-July), they were the first cohorts susceptible to show a compensatory response in recruitment 3 years after mass removal. CPUE and BPUE of pearl dace (Lake Mastigou), lake chub (Lake Rimouski), golden shiner (Lake Des Iles), longnose sucker, common shiner, and fallfish (Lake Cinq Doigts) were only compared with t tests because they occurred in only one lake or their abundance was too low. Normality was tested before analysis with a Kolmogorov–Smirnov (Lilliefors) test, and the homogeneity of variances was tested with an F_{max} test (Sokal and Rohlf 1981). When the assumptions of normality and (or) homogeneity of variances were not met, the data were $\log(x + 1)$ transformed. The data were not always normally distributed and (or) the variances homogeneous; in these cases, we assumed that departures from these assumptions had no marked effect on the t test significance levels (Sokal and Rolf 1981).

Age and growth

White sucker age determination was done as described by Beamish (1973). A Jem Saw 45™ (model #20-037, Raytech Industries, Middlefield, CT 06457) was used to cut transverse sections of the first three pectoral fin rays, which were then fixed to a microscope slide with Cytoseal 60™ (Stevens Scientific, Kalamazoo, Mich.). Two independent readings were done by a single reader. When the first two readings differed, a third reading was done. For brook trout, scales were mounted between acetate sheets directly in the field (Power 1964). Age was estimated by two readers. When the first two readings differed, two other readings were completed; the sample was discarded if there was still no agreement. For each white sucker and brook trout population, a maximum of 130 individuals were used for age determination. All specimens from the least abundant size classes (i.e., smaller and larger fish) were used; the subsample was completed with a fixed number of fish randomly selected from the other size classes (at 10-mm intervals). Age structures of these populations were determined by assigning to each length class the number of non-aged individuals in the same proportion as the aged ones. We compared age structures of white sucker and brook trout populations before (or the year of) and after mass removal using a Kolmogorov–Smirnov test.

To evaluate growth compensation in white sucker and brook trout, we first tested for the effect of mass removal, lake, and age on length of individuals with a mixed model ANOVA. We also tested for differences in slope of the length-at-age relationships (*i*) between the year of and 3 years after mass removal in lakes Mastigou, Claudette, and Rimouski and (*ii*) between 1 year before and 3 years after mass removal in lakes des Iles and Cinq Doigts. The relationships between log(length) and log(age + 1) were fitted to a general linear model (GLM) before testing for differences in slope. The slopes of the length–age relationship did not differ for any of brook trout populations ($p > 0.05$). Therefore, we tested for difference in mean adjusted length with an analysis of covariance (ANCOVA) (Packard and Broadman 1987). Brook trout data were adjusted for grand mean ages of 2.8, 2.5, 2.0, 3.1, and 2.7 years in lakes Mastigou, Claudette, Rimouski, des Iles, and Cinq Doigts, respectively, with an ANCOVA. The same length ranges were used for growth comparison in lakes Mastigou and Claudette because of differences in the types of gillnet used.

Reproductive traits

The fecundity of female white sucker and brook trout was estimated by proportion using the mean weight of three samples of 25 eggs and the total egg mass (Snyder 1983). Eggs were separated from ovarian connective tissue, air dried for 48 h, and weighed (±0.01 mg). The accuracy of this method was ±5% when compared with total counts made on 10% of the samples. Brook trout fecundity was not estimated in Lake Cinq Doigts because of the low sample size.

To evaluate the fecundity compensation in white sucker and brook trout, we first tested for the effect of mass removal, lake, and length of females on fecundity with a mixed model ANOVA. We also tested for differences in the slopes of the length–fecundity relationships the year of mass removal and 3 years after mass removal using the GLM procedure. As the slope of the relationships between log(fecundity) and length did not differ between years for brook trout and white sucker in lakes Mastigou, Claudette, and

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Table 2. Biomass (kg·ha^{-1}) of white sucker removed on their spawning grounds during the 3 years of biomanipulation in the five study lakes (1995 to 1997 in lakes Mastigou, Claudette, and Rimouski; 1996 to 1998 in lakes des Iles and Cinq Doigts).

Lake	Surface area (ha)	Biomass (kg·ha^{-1})			
		Year 1	Year 2	Year 3	Total
Mastigou	177	16.6	7.3	7.3	31.3
Claudette	110	13.8	6.3	3.1	23.2
Rimouski	114	18.3	4.4	3.0	25.7
Des Iles	347	7.4	4.6	2.1	14.2
Cinq Doigts	615	5.6	6.0	3.4	15.0

Note: The biomass of white sucker removed decreased significantly 3 years after biomanipulation in all lakes ($p < 0.05$).

Rimouski ($p > 0.05$), we tested for differences in adjusted mean fecundity using an ANCOVA (Packard and Broadman 1987). Data were adjusted for grand mean lengths of 250.5 mm, 279.9 mm, and 368.4 mm for white sucker and 275.3 mm, 213.6 mm, and 255.8 mm for brook trout in lakes Mastigou, Claudette, and Rimouski, respectively.

To evaluate the impact of white sucker removal on length and age at maturity of white sucker and brook trout, we first tested for the effect of mass removal and lake on length of mature individuals with a mixed model ANOVA. We also used a *t* test to compare the mean length and age at maturity of white sucker and brook trout between the year of mass removal and 3 years after mass removal in lakes Mastigou, Claudette, and Rimouski. These comparisons were made between 1 year before and 3 years after mass removal only for brook trout in Lake des Iles. The sample sizes for brook trout males in Lake Rimouski and for brook trout males and females in Lake Cinq Doigts were too low to allow comparisons. To compute mean length and age at maturity, we attributed the sex ratio of mature individuals to the immature ones. The age of each white sucker captured during spring sampling was estimated from the log(length) – log(age + 1) relationship obtained from gillnet sampling. When assumptions of normality and (or) homogeneity of variances were not met, the data were log(x + 1) transformed. All statistical analyses were performed with SYSTAT version 7.0 software (SPSS Science, Chicago, Ill.).

Results

White sucker removal

The total biomass of white sucker removed from the five studied lakes during 3 years of biomanipulation ranged from 2552 kg to 9225 kg (Table 2). Lake Mastigou experienced the highest white sucker removal per hectare, whereas the two larger lakes (des Iles and Cinq Doigts) had the lowest (Table 2). The biomass of white sucker removed decreased significantly 3 years after biomanipulation in all lakes ($p < 0.05$).

Fish species response to white sucker removal

Fish abundance

The two-way ANOVA revealed significant effects of both mass removal and lake, as well as their interactions on CPUE of white sucker (mass removal, $F = 14.04$, $p < 0.001$; lake, $F = 10.82$, $p < 0.001$; mass removal × lake, $F = 5.28$, $p < 0.005$; $n = 96$ gillnets). In contrast, only lake and mass removal × lake effects were significant on BPUE of white sucker (mass removal, $F = 2.03$, $p > 0.05$; lake, $F = 18.58$, $p < 0.001$; mass removal × lake, $F = 4.16$, $p < 0.001$; $n = 96$ gillnets). The mean CPUE and BPUE of white sucker decreased significantly 3 years after mass removal in Lake Mastigou ($t = 4.17$ and 4.25, respectively; $p < 0.001$; Figs. 1*a*, 1*b*); CPUE decreased by 71.5% and BPUE by 64.3%. Although not significant, CPUE of white sucker also tended to decrease 3 years after mass removal in lakes Claudette (–36.3%), Rimouski (–18.0%), and Cinq Doigts (–45.0%) ($t = 1.42$, 0.81, and 1.53, respectively; $p > 0.05$; Fig. 1*a*). There was no significant difference in mean white sucker CPUE in Lake des Iles (+7.1%) and BPUE in lakes Claudette (–17.9%), Rimouski (+8.3%), des Iles (+21.2), and Cinq Doigts (–1.6%) 3 years after mass removal ($t = 0.28$, 0.82, 0.35, 0.74, and 0.06, respectively; $p > 0.05$; Figs. 1*a*, 1*b*).

The two-way ANOVA showed that lake and mass removal × lake effects were significant on CPUE and BPUE of 2+ white sucker (CPUE: mass removal, $F = 2.60$, $p > 0.05$; lake, $F = 8.19$, $p < 0.001$; mass removal × lake, $F = 4.77$, $p < 0.01$; BPUE: mass removal, $F = 1.29$, $p > 0.05$; lake, $F = 9.37$, $p < 0.001$; mass removal × lake, $F = 3.71$, $p < 0.01$; $n = 98$ gillnets). Mean CPUE and BPUE of 2+ white sucker increased significantly 3 years after mass removal in Lake Rimouski ($t = 2.95$ and 3.10, respectively; $p < 0.05$; Figs. 1*c*, 1*d*). The opposite response was observed in Lake Cinq Doigts, where mean CPUE of 2+ white sucker decreased significantly 3 years after mass removal although mean BPUE did not change significantly ($t = 3.19$ and 2.09, respectively; $p < 0.01$ and $p > 0.05$, respectively; Figs. 1*c*, 1*d*). There was no difference in mean CPUE and BPUE of 2+ white sucker 3 years after mass removal in lakes Mastigou, Claudette, and des Iles (CPUE: $t = 0.21$, 1.14, and 1.20, respectively; BPUE: $t = 0.03$, 0.35, and 0.90, respectively; $p > 0.05$; Figs. 1*c*, 1*d*).

The two-way ANOVA revealed that only lake effect was significant on CPUE and BPUE of brook trout (CPUE: mass removal, $F = 2.67$, $p > 0.05$; lake, $F = 25.00$, $p < 0.001$; mass removal × lake, $F = 0.67$, $p > 0.05$; BPUE: mass removal, $F = 1.66$, $p > 0.05$; lake, $F = 8.64$, $p < 0.001$; mass removal × lake, $F = 0.55$, $p > 0.05$; $n = 96$ gillnets). Mean CPUE and BPUE of brook trout were not significantly affected by mass removal of white suckers in lakes Mastigou, Claudette, Rimouski, des Iles, and Cinq Doigts (CPUE: $t = 1.07$, 0.91, 1.54, 0.19, and 0.84, respectively; BPUE: $t = 0.64$, 0.25, 0.24, 1.38, and 1.64, respectively; $p > 0.05$; Figs. 2*a*, 2*b*). However, the two-way ANOVA revealed significant effects of both mass removal and lake, as well as their interactions on CPUE and BPUE of 1+ brook trout (CPUE: mass removal, $F = 26.57$, $p < 0.001$; lake, $F = 9.71$, $p < 0.001$; mass removal × lake, $F = 7.39$, $p < 0.001$; BPUE: mass removal, $F = 29.87$, $p < 0.001$; lake, $F = 5.72$, $p < 0.001$; mass removal × lake, $F = 5.50$, $p < 0.01$; $n = 98$ gillnets). The mean CPUE and BPUE of 1+ brook trout were significantly higher after mass removal in lakes Mastigou, Claudette, and Rimouski (CPUE: $t = 3.99$, 2.77, and 3.69, respectively; BPUE: $t = 3.93$, 2.16, and 3.69, respectively; $p < 0.05$; Figs. 2*c*, 2*d*). There was no significant difference in mean CPUE and BPUE of 1+ brook trout between 1 year before and 3 years after mass removal in lakes Des Iles and Cinq Doigts (CPUE: $t = 0.77$ and 0.77, respectively; BPUE: $t = 0.59$ and 0.67, respectively; $p > 0.05$; Figs. 2*c*, 2*d*).

There was no significant difference between mean CPUE and BPUE of pearl dace, lake chub, golden shiner, common

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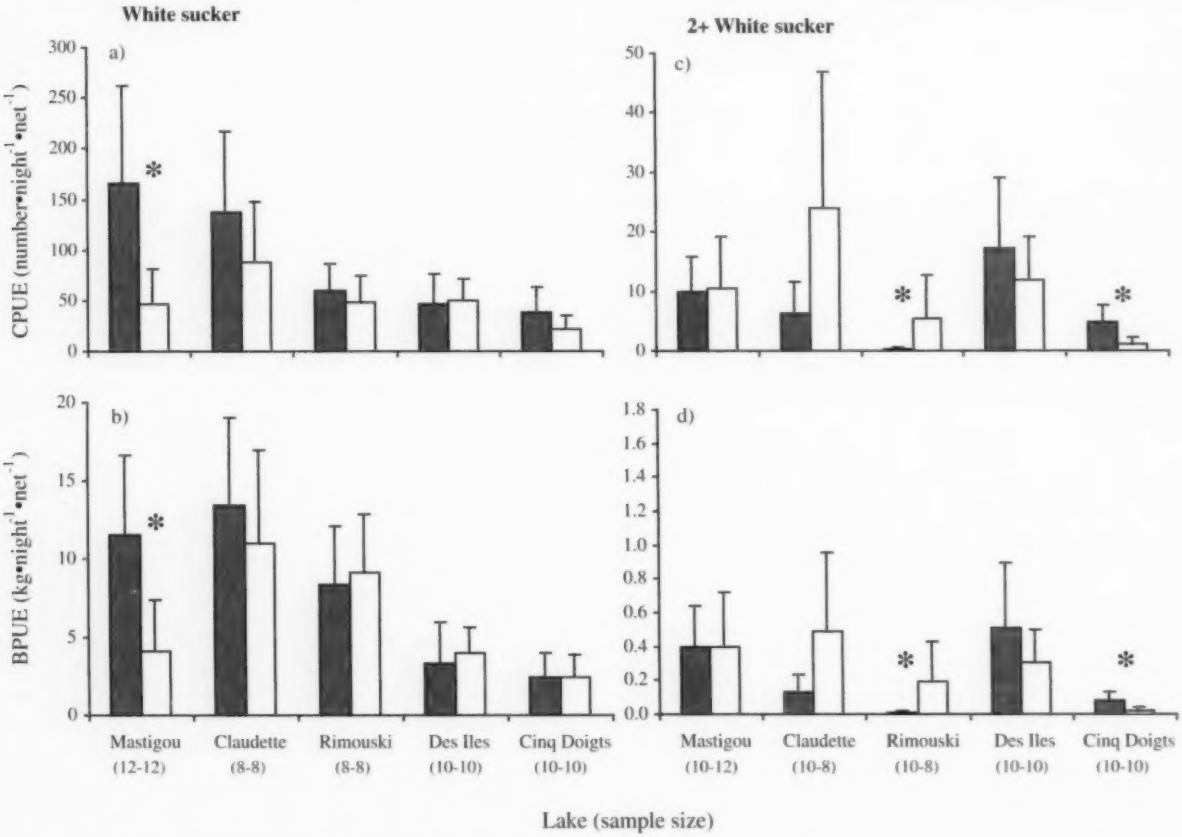
Fig. 1. Mean catch and biomass per unit of effort (CPUE and BPUE ± 1 standard deviation) of white sucker populations (*a* and *b*, all age classes) and 2+ white sucker (*c* and *d*). Solid bars, before or in the year of white sucker mass removal; open bars, 3 years after white sucker mass removal. CPUE and BPUE with an asterisk are significantly different as determined by a *t* test (white sucker population, $p < 0.001$; 2+ white sucker, $p < 0.05$).



shiner, fallfish, and longnose sucker before (or the year of) and after mass removal (CPUE (number·night^{-1}·net^{-1}) ± standard deviation (SD) and BPUE (kg·night^{-1}·net^{-1}) ± SD (number of gillnets in parentheses)): pearl dace, 3.33 ± 5.85 and 0.05 ± 0.10 (24); lake chub, 18.33 ± 22.26 and 0.34 ± 0.40 (18); golden shiner, 5.80 ± 7.14 and 0.09 ± 0.10 (20); longnose sucker, 5.90 ± 8.93 and 0.28 ± 0.37 (20); common shiner, 4.6 ± 5.6 and 0.12 ± 0.16 (20); fallfish, 64.60 ± 45.37 and 1.95 ± 1.32 (20) ($p > 0.05$).

Age and growth

White sucker age structure remained unchanged 3 years after mass removal in Lake Mastigou (K–S = 0.08; $p > 0.05$; Fig. 3*a*), whereas significant changes occurred in lakes Claudette, Rimouski, des Iles, and Cinq Doigts (K–S = 0.22, 0.24, 0.25, and 0.16, respectively; $p < 0.01$; Figs. 3*b*, 3*c*, 3*d*, 3*e*). The most striking change was an increase in the proportion of 2+ to 4+ individuals following mass removal (Fig. 3).

Brook trout age structure showed a significant shift towards younger cohorts after white sucker mass removal in lakes Mastigou and Claudette (K–S = 0.27 and 0.28, respectively; $p < 0.001$; Figs. 4*a*, 4*b*). Although not significant, the same trend was observed in Lake Rimouski (K–S = 0.22; $p > 0.05$; Fig. 4*c*). The opposite response was observed in Lake des Iles, where brook trout age structure shifted to older individuals after white sucker mass removal (K–S = 0.39; $p < 0.01$; Fig. 4*d*). No significant change was observed for Lake Cinq Doigts following mass removal (K–S = 0.25; $p > 0.05$; Fig. 4*e*).

The three-way ANOVA revealed significant effects of mass removal, lake, and age, as well as their interactions on white sucker length (mass removal, $F = 43.09$, $p < 0.001$; lake, $F = 106.12$, $p < 0.001$; age, $F = 3790.16$, $p < 0.001$; mass removal × lake, $F = 21.56$, $p < 0.001$; mass removal × age, $F = 13.23$, $p < 0.001$; $n = 1140$ fish). The slope of the length-at-age relationship of white sucker was significantly higher 3 years after white sucker removal in lakes Mastigou, Claudette, des Iles, and Cinq Doigts, whereas it was significantly lower in Lake Rimouski ($F = 4.75$, 26.26, 8.45, 8.45, and 15.64, respectively; $p < 0.05$; Fig. 5*a*). Although not testable because of the significant difference in slope, the intercept showed a mean increase of 12.7% following mass removal (1.73 ± 0.03 in 1995 versus 1.95 ± 0.02 in 1997), suggesting a growth increase in young individuals. The three-way ANOVA also showed significant effects of mass removal, lake, and age, as well as their interactions on brook

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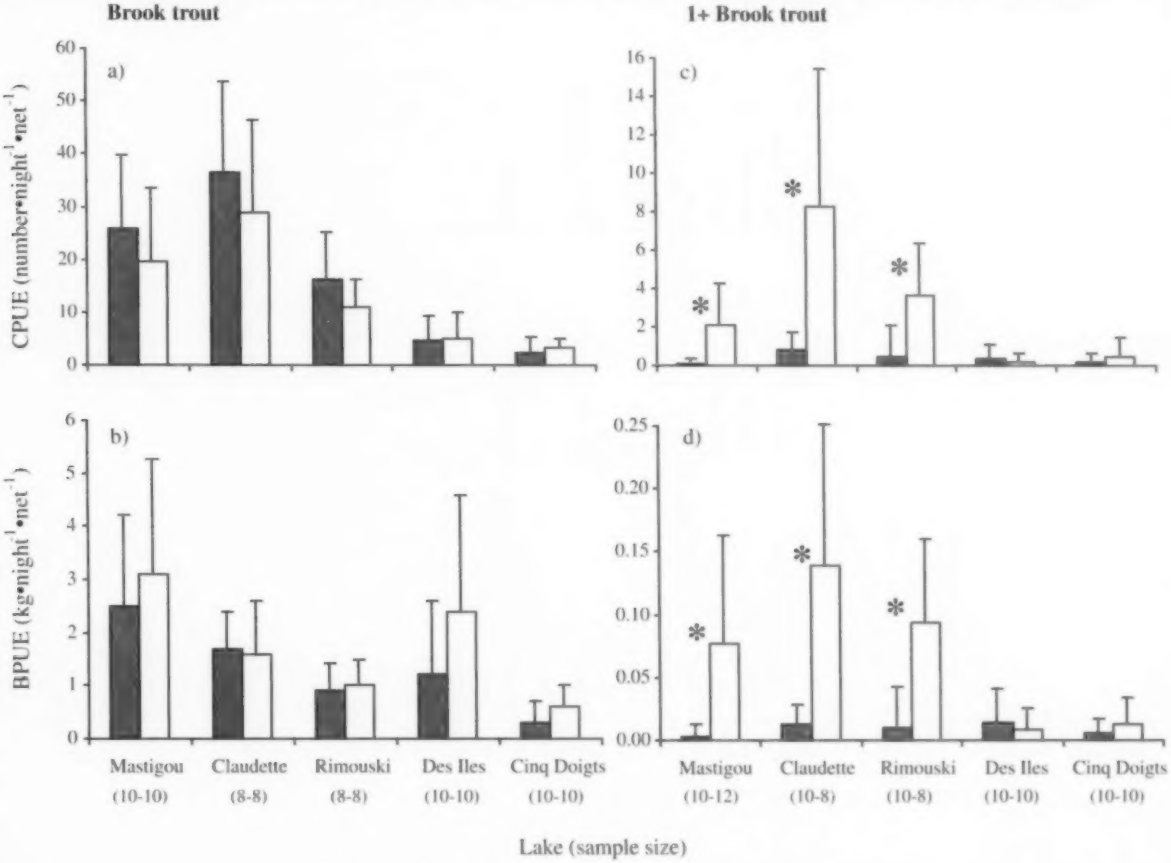
Fig. 2. Mean catch and biomass per unit of effort (CPUE and BPUE ± 1 standard deviation) of brook trout populations (*a* and *b*, all age classes) and 1+ brook trout (*c* and *d*). Solid bars, before or in the year of white sucker mass removal; open bars, 3 years after white sucker mass removal. CPUE and BPUE with an asterisk are significantly different as determined by a *t* test ($p < 0.05$).



trout length (mass removal, $F = 20.97$, $p < 0.001$; lake, $F = 411.94$, $p < 0.001$; age, $F = 2546.10$, $p < 0.001$; mass removal × lake, $F = 3.83$, $p < 0.01$; mass removal × age, $F = 4.50$, $p < 0.05$; $n = 652$ fish). The mean adjusted length of brook trout increased significantly 3 years after white sucker mass removal in lakes Mastigou, Claudette, and des Iles ($F = 17.99$, 8.24, and 10.56, respectively, $p < 0.005$; Fig. 5*b*). Mean adjusted length of brook trout did not vary after mass removal in lakes Rimouski and Cinq Doigts ($F = 0.43$ and 0.01, respectively, $p > 0.05$; Fig. 5*b*).

Reproductive traits

The three-way ANOVA revealed significant effects of mass removal, lake, and length, as well as interaction between mass removal and lake on white sucker fecundity (mass removal, $F = 31.74$, $p < 0.001$; lake, $F = 4.70$, $p < 0.05$; length, $F = 114.20$, $p < 0.001$; mass removal × lake, $F = 3.85$, $p < 0.05$; mass removal × length, $F = 0.04$, $p > 0.05$; $n = 110$ females). White sucker females of lakes Mastigou and Claudette experienced a significant increase in mean adjusted fecundity 3 years after white sucker mass removal ($F = 12.34$ and 17.10, respectively, $p < 0.005$; Fig. 6*a*). Although not significant, the same trend was observed in Lake Rimouski ($F = 3.13$, $p > 0.05$; Fig. 6*a*). The two-way ANOVA showed that only the effect of lake was significant on both mean length and age at maturity of white sucker males (length at maturity: mass removal, $F = 2.57$, $p > 0.05$; lake, $F = 44.59$, $p < 0.001$; mass removal × lake, $F = 0.81$, $p > 0.05$; age at maturity: mass removal, $F = 0.24$, $p > 0.05$; lake, $F = 96.34$, $p < 0.001$; mass removal × lake, $F = 1.89$, $p > 0.05$; $n = 138$ individuals). For white sucker females, the two-way ANOVA revealed significant effects of mass removal and lake on mean length at maturity and a significant effect of lake only on mean age at maturity (length at maturity: mass removal, $F = 16.26$, $p < 0.001$; lake, $F = 108.54$, $p < 0.001$; mass removal × lake, $F = 0.88$, $p > 0.05$; age at maturity: mass removal, $F = 0.08$, $p > 0.05$; lake, $F = 312.91$, $p < 0.001$; mass removal × lake, $F = 2.53$, $p > 0.05$; $n = 232$ individuals). Mean length at maturity of white sucker females showed a significant increase after mass removal in lakes Mastigou, Claudette, and Rimouski ($t = 2.67$, 2.08, and 2.39, respectively; $p < 0.05$; Fig. 7*c*), whereas males experienced no significant change ($t = 0.11$, 1.09, and 1.48, respectively; $p > 0.05$; Fig. 7*a*). Males of Lake Rimouski experienced a significant decrease in their mean age at maturity ($t = 3.48$; $p < 0.005$; Fig. 7*b*), whereas no difference was observed in

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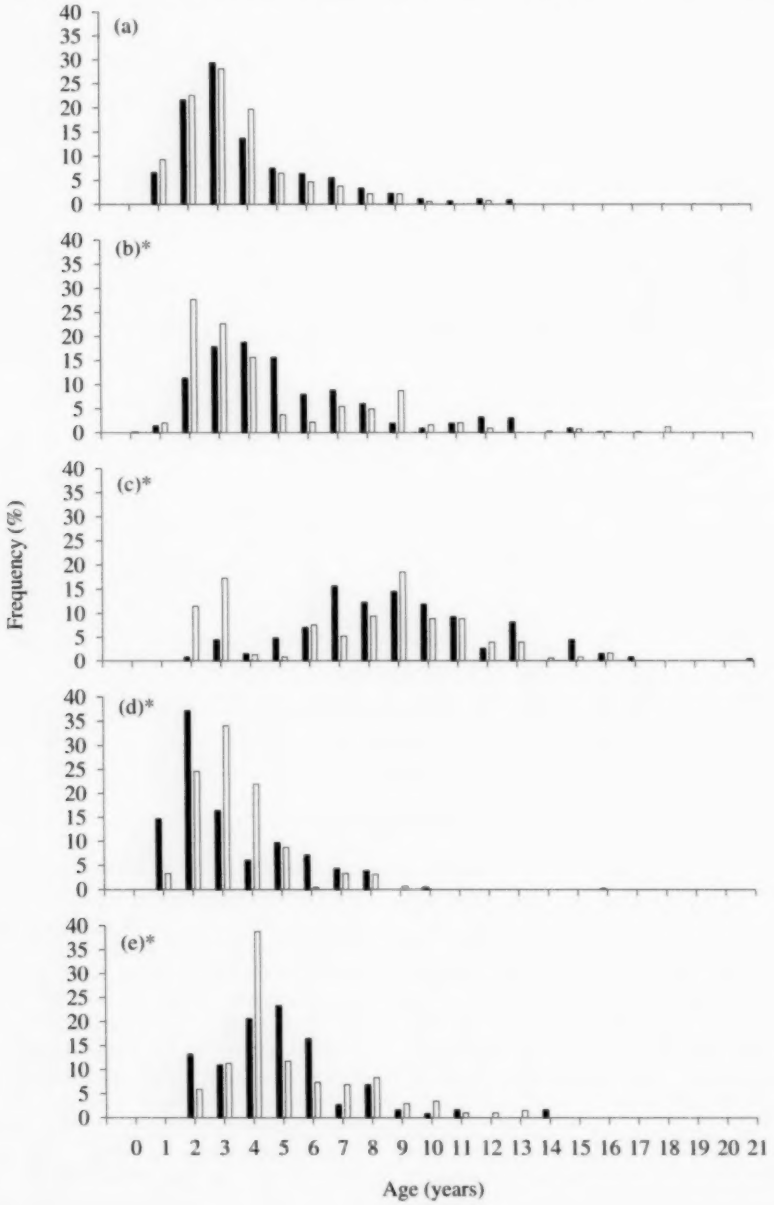
Fig. 3. Age frequency distribution of white sucker populations. Solid bars, before or in the year of white sucker mass removal, n = 453, 564, 269, 463, and 364 in lakes Mastigou, Claudette, Rimouski, des Iles, and Cinq Doigts, respectively; open bars, 3 years after white sucker mass removal, n = 559, 697, 383, 484, and 204 in lakes Mastigou, Claudette, Rimouski, des Iles, and Cinq Doigts, respectively. Age frequency distributions with an asterisk are significantly different as determined by a Kolmogorov–Smirnov test ($p < 0.05$).



lakes Mastigou and Claudette (t = 0.21 and 1.05, respectively; $p > 0.05$; Fig. 7*b*). Mean age at maturity of white sucker females showed no significant difference 3 years after mass removal in lakes Mastigou, Claudette, and Rimouski (t = 0.69, 1.55, and 1.66, respectively; $p > 0.05$; Fig. 7*d*).

The three-way ANOVA revealed significant effects of lake and length, as well as interaction between mass removal and lake on brook trout fecundity (mass removal, F = 0.13, $p > 0.05$; lake, F = 208.49, $p < 0.001$; length, F = 199.29, $p < 0.001$; mass removal × lake, F = 13.83, $p < 0.001$; mass removal × length, F = 0.32, $p > 0.05$; n = 194 females). Brook trout females showed a significant increase in mean adjusted fecundity 3 years after mass removal only in Lake Mastigou (F = 25.94; $p < 0.001$; Fig. 6*b*). The opposite response was observed in Lake Claudette (F = 9.82; $p < 0.005$; Fig. 6*b*), and there was no significant difference in Lake Rimouski

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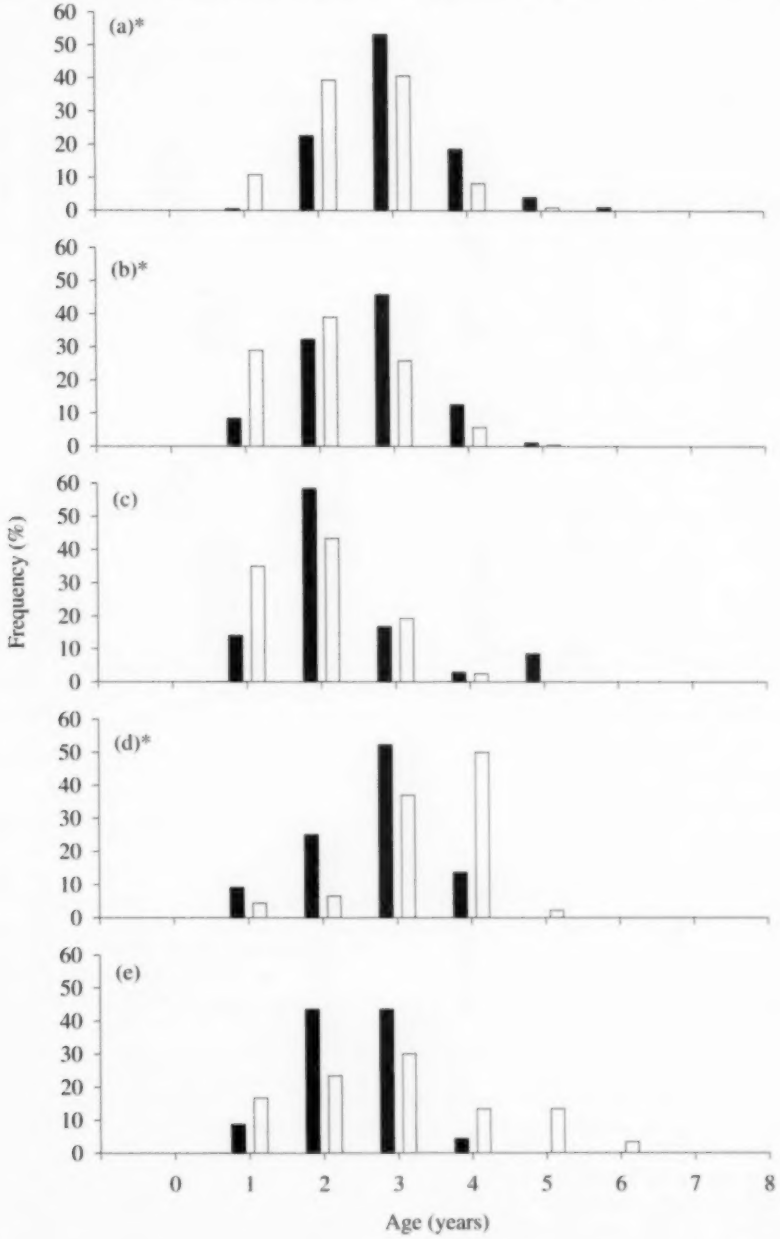
Fig. 4. Age frequency distributions of brook trout population. Solid bars, before or in the year of white sucker mass removal, n = 199, 96, 36, 44, and 23 in lakes Mastigou, Claudette, Rimouski, des Iles, and Cinq Doigts, respectively; open bars: 3 years after white sucker mass removal, n = 231, 228, 83, 46, and 30 in lakes Mastigou, Claudette, Rimouski, des Iles, and Cinq Doigts, respectively. Age frequency distributions with an asterisk are significantly different as determined by a Kolmogorov–Smirnov test ($p < 0.05$).



(F = 2.42; $p > 0.05$; Fig. 6*b*). We also observed a significant decrease in the slope of the relationship between length and fecundity in Lake des Iles (0.005 ± 0.001 in 1995 and 0.003 ± 0.001 in 1998; F = 5.00, $p < 0.05$). Although not testable because of the significant difference in slope, the intercept showed an 80% increase following mass removal in Lake des Iles (1.23 ± 0.32 in 1995 versus 2.29 ± 0.25 in 1998), suggesting an increase in fecundity of small individuals. The two-way ANOVA showed that only the effect of lake was significant on mean length at maturity of brook trout males, whereas lake and the interaction between mass removal and lake had significant effects on their mean age at maturity (length at maturity: mass removal, F = 0.24, $p > 0.05$; lake, F = 39.45, $p < 0.001$; mass removal × lake, F = 1.83, $p >$

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Fig. 5. Slope (±1 standard error (SE)) and R^2 (%) of the length-at-age relationship of white sucker (*a*) and mean adjusted length (±1 standard deviation) of brook trout (*b*) populations. Solid bars, before or in the year of white sucker mass removal; open bars, 3 years after white sucker mass removal. Brook trout data were adjusted for grand mean ages of 2.8, 2.5, 2.0, 3.1, and 2.7 years in lakes Mastigou, Claudette, Rimouski, des Iles, and Cinq Doigts, respectively. Slope and mean adjusted length with an asterisk are significantly different ($p < 0.05$).

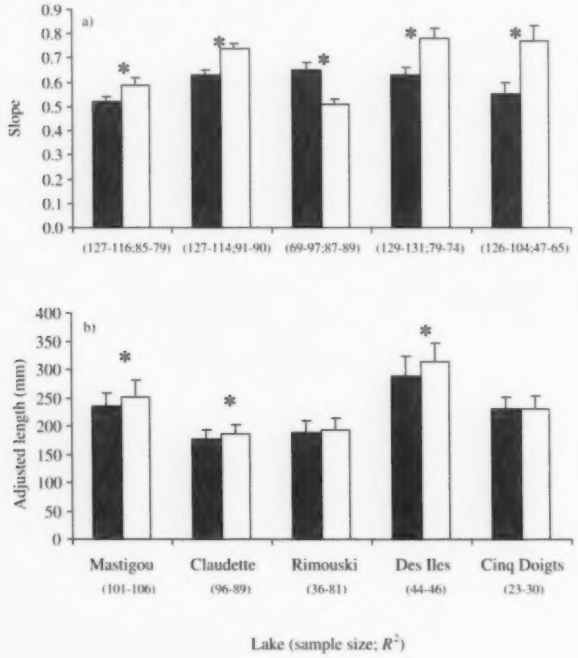
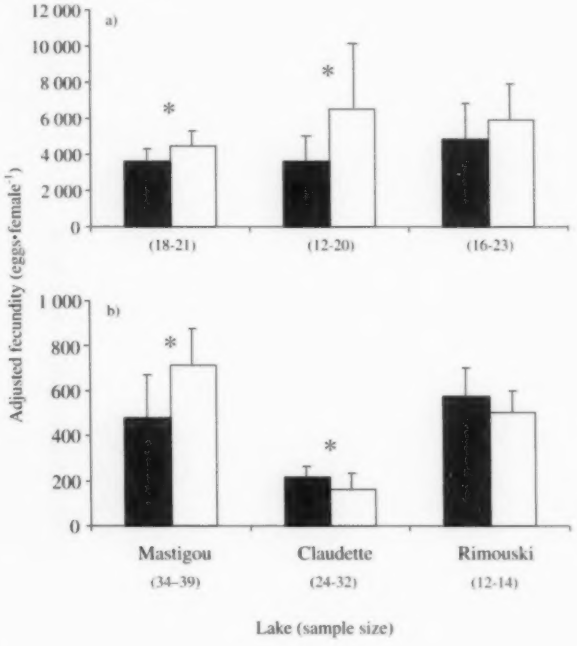


Fig. 6. Mean adjusted fecundity (±1 standard deviation) for white sucker (*a*) and brook trout (*b*) populations. Solid bars, before white sucker mass removal; open bars, 3 years after white sucker mass removal. Data were adjusted for grand mean lengths of 250.5 mm, 279.9 mm, and 368.4 mm for white sucker and 275.3 mm, 213.6 mm, and 255.8 mm for brook trout in lakes Mastigou, Claudette, and Rimouski, respectively. Fecundity with an asterisk are significantly different as determined by an ANCOVA ($p < 0.005$).



0.05; age at maturity: mass removal, $F = 2.25$, $p > 0.05$; lake, $F = 3.23$, $p < 0.05$; mass removal × lake, $F = 3.19$, $p < 0.05$; $n = 179$ individuals). For brook trout females, the two-way ANOVA showed significant effects of mass removal and lake, as well as their interaction on mean length at maturity, and a significant effect of lake on their mean age at maturity (length at maturity: mass removal, $F = 6.12$, $p < 0.05$; lake, $F = 78.90$, $p < 0.001$; mass removal × lake, $F = 2.93$, $p < 0.05$; age at maturity: mass removal, $F = 0.53$, $p > 0.05$; lake, $F = 6.30$, $p < 0.001$; mass removal × lake, $F = 1.92$, $p > 0.05$; $n = 298$ individuals). Mean length at maturity of brook trout females showed a significant increase 3 years after white sucker mass removal in Lake des Iles ($t = 1.77$; $p < 0.05$; Fig. 8*c*). There was no significant difference in brook trout length at maturity 3 years after mass removal for males in lakes Mastigou, Claudette, and des Iles and for females in lakes Mastigou, Claudette, and Rimouski (males, $t = 1.44$, 0.42, and 0.99, respectively; females, 1.69, 0.88, and 0.25, respectively; $p > 0.05$; Figs. 8*a*, 8*c*). Mean age at maturity decreased significantly in Lake Mastigou for both males and females ($t = 4.07$ and 2.32, respectively; $p < 0.05$; Figs. 8*b*, 8*d*), whereas no differences were observed in lakes Claudette and des Iles for males or in lakes Claudette, Rimouski, and des Iles for females (males, $t = 1.62$ and 0.61, respectively; females, $t = 0.72$, 0.62, and 1.77, respectively; $p > 0.05$; Figs. 8*b*, 8*d*).

Discussion

White sucker removal

CPUE and BPUE of white sucker indicate that mass removal was most efficient in lakes Mastigou and Claudette (with decreases in CPUE of 72% and 36% and BPUE of 64% and 18%, respectively) and negligible in the other three lakes (decrease in CPUE between 0% and 45% but no change in BPUE). Johnson (1977) and Hayes et al. (1992), who removed 34 kg·ha^{-1} and 45 kg·ha^{-1}, respectively, of white sucker in the first year of a biomanipulation, decreased the initial estimated adult standing crop by 85% (after 1 year of mass removal) and the initial CPUE by 80% (after 2 years of mass removal) in lakes of 245 ha and 38.1 ha, respectively. The higher white sucker age at maturity in Lake Rimouski (11–17 years) probably decreased the efficiency of mass removal because a lower proportion of the population migrate to spawning grounds in this case. The significant interactions between mass removal and lake in the two-way ANOVA tests for effects on CPUE and BPUE of white sucker indicate that the effect of mass removal was not the same in all lakes.

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Fig. 7. Mean length and age at maturity (±1 standard deviation) of white sucker males (*a* and *b*) and females (*c* and *d*). Solid bars, before white sucker mass removal; open bars, 3 years after white sucker mass removal. Mean length and age with an asterisk are significantly different as determined by a *t* test.

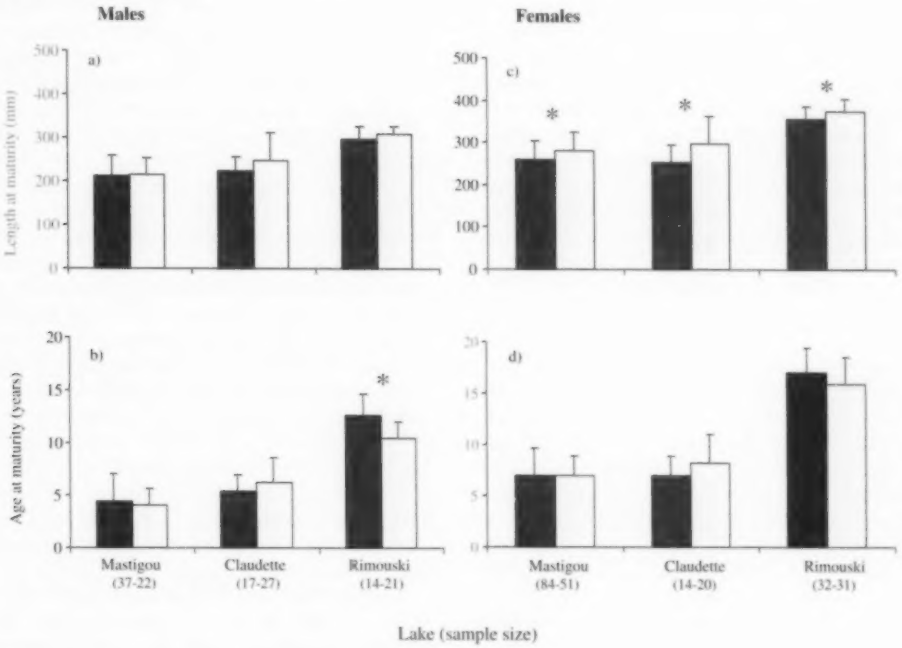
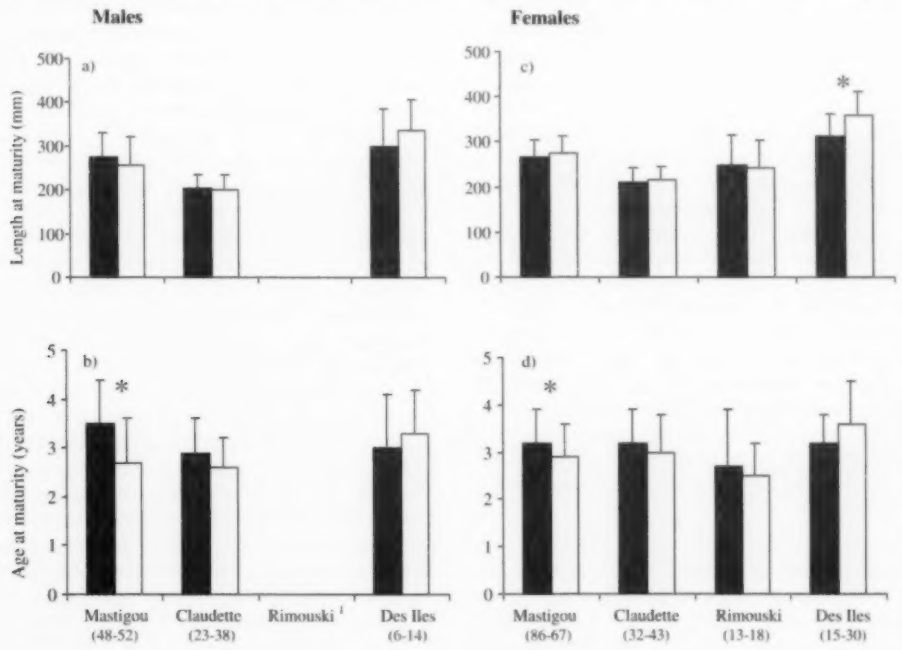


Fig. 8. Mean length and age at maturity (±1 standard deviation) of brook trout males (*a* and *b*) and females (*c* and *d*). Solid bars, before white sucker mass removal; open bars, 3 years after white sucker mass removal. Mean length and age with an asterisk are significantly different as determined by a *t* test. [1] The sample size of males in Lake Rimouski was too low to allow comparisons.



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Fish species response to white sucker removal

Fish abundance

Mass removal of adult fish should result in an increase in recruitment of all species because of a competitive release (Magnan et al. 1990; Meronek et al. 1996). The significant interactions between mass removal and lake in two-way ANOVA tests for effects on CPUE and BPUE of 2+ white sucker indicate that the effect of mass removal was not the same in all lakes. The lack of a significant increase in mean CPUE and BPUE of 2+ white sucker 3 years after mass removal in Lake Mastigou is probably related to the mass removal of reproducing individuals 3 years before, which was higher than in other lakes. In contrast, the significant increase in 2+ white sucker abundance (CPUE and BPUE) 3 years after mass removal in Lake Rimouski and the trend observed in Lake Claudette suggest a compensatory response in white sucker recruitment 3 years after mass removal. This improved recruitment may have contributed to the absence of a significant decrease in mean total CPUE and BPUE after mass removal in lakes Rimouski and Claudette. The lack of a significant increase in mean total brook trout CPUE and BPUE after mass removal is probably the result of our short-term monitoring after biomanipulation (3 years). Venne and Magnan (1995) observed that CPUE of young-of-the-year (YOY) was 93% lower in the five lakes containing white sucker than in five allopatric populations, suggesting the presence of a competitive bottleneck for YOY trout occurring somewhere before the end of May. Because mass removal was always completed after this period in our experimental lakes, survival could only be improved the second year of biomanipulation in response to the decrease in white sucker abundance during the first year of mass removal. The increase in 1+ brook trout abundance (CPUE and BPUE) 3 years after mass removal in lakes Mastigou, Claudette, and Rimouski supports this interpretation. Bias owing to differences in gillnets used in 1995 and 1997 in lakes Mastigou and Claudette could not explain the significant increase of 1+ brook trout because the nets were similarly selective for these individuals, with panels of 13 m and 15 m, respectively, for 2.5–3.2 mm stretched meshes. Furthermore, the significant increase in CPUE of 1+ brook trout observed in Lake Rimouski was obtained with identical gillnets. Mass removal was probably too low in lakes des Iles and Cinq Doigts to result in an increase in 1+ brook trout. The significant interactions between mass removal and lake in the two-way ANOVA tests for effects on CPUE and BPUE of 1+ brook trout also indicate that the effect of mass removal was not the same in all lakes. Johnson (1977) and Schneider and Crowe (1980) also observed an increased recruitment of yellow perch (*Perca flavescens*) after white sucker mass removal. In a similar biomanipulation, Hayes et al. (1992) did not observe any increase in YOY yellow perch abundance.

Age and growth

The increased proportion of 2+ to 4+ white suckers in lakes Claudette, Rimouski, des Iles, and Cinq Doigts 3 years after mass removal may result from a difference in vulnerability to mass removal between immature and mature individuals. Mean age at maturity is usually more than 4 years in white sucker (Duchesne and Magnan 1997; this study). The significant shift in brook trout age structure towards younger fish in lakes Mastigou and Claudette as well as the trend observed in Lake Rimouski are also consistent with a compensatory recruitment response in these lakes. Our results support the conclusions that decreases in intraspecific competition for food and (or) space should result in better recruitment (Langeland 1986; Amundsen et al. 1993).

The increase in the slope of the length-at-age relationship of white sucker in four of the five lakes indicates that the growth response to mass removal was more important in older individuals than in younger ones. The age–length relationship (not presented here; see Brodeur 2000) showed increases in length for both young and old individuals. The significant increase in slope coupled with the increase in intercept thus suggests more important growth compensation in small individuals. Johnson (1977) and Schneider and Crowe (1980) also observed a similar positive growth response in older white sucker (3+) following similar biomanipulations. It is possible that growth is already maximal in white sucker <3+ before biomanipulation, explaining the more important response of older fish. Changes observed in white sucker length frequency distribution (not presented here; see Brodeur 2000) support the compensatory growth response of individuals and are typical of fish populations experiencing strong exploitation (Hanson et al. 1983; Langeland 1986; Amundsen et al. 1993).

Chen and Harvey (1995) suggested that white sucker growth may be constrained by population density and food supply. However, the growth response in white sucker was not clearly related to removal intensity because all white sucker populations experienced comparable growth increases. Interannual variations in environmental factors such as temperature could have had an impact on this positive response. It is also possible that there is a threshold beyond which additional reductions in abundance could cause minimal increases in white sucker growth. Donald and Alger (1989) obtained such a growth response in an exploited brook trout population even though the total density of the population did not change significantly.

Compared with that of white sucker, the compensatory response in brook trout growth seemed to be related to removal intensity. The significant interactions between mass removal and lake in the two-way ANOVA tests for effects on brook trout length indicate that the effect of mass removal was not the same in all lakes. Furthermore, the lake-by-lake comparisons showed significant increases in the two lakes that experienced the highest white sucker removal (lakes Mastigou and Claudette). The brook trout growth increase observed in the present study probably resulted from an increase in food availability after mass removal, particularly of benthic invertebrates, which are important food items for white sucker in sympatric lakes (Magnan 1988; Tremblay and Magnan 1991; Lacasse and Magnan 1992). A positive growth response was also observed in brook trout of Lake des Iles, which experienced a low mass removal. However, this lake is the only one where the brook trout population exhibited a significant increase in the proportion of older individuals after mass removal. Hayes et al. (1992), Johnson (1977), and Schneider and Crowe (1980) observed such a compensatory response in yellow perch after significant white sucker mass removal. The length frequency distributions of

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brook trout (not shown here; see Brodeur 2000) also support the compensatory growth response of individuals.

Reproductive traits

White sucker in lakes Mastigou and Claudette exhibited increases in fecundity following mass removal that was independent of the growth increase in adults. This is consistent with a greater energy investment in egg production after a reduction of intraspecific competition: better conditions for growth produced a higher fecundity in lake whitefish (*Coregonus clupeaformis*) and lake trout (*Salvelinus namaycush*) (Healey 1978) as well as in roach (*Rutilus rutilus*; Burrough and Kennedy 1979) after an intensive exploitation.

Brook trout exhibited increased fecundity in lakes Mastigou and des Iles but not in Lake Claudette, where mass removal was significant. The significant increase in growth rate of brook trout in Lake des Iles may also have contributed to increased fecundity through a surplus in energy. Significant decreases of brook trout fecundity in Lake Claudette remain unexplained because growth also increased in this population. However, the increase in adjusted mean length of brook trout from Lake Claudette (4.2%) was lower than those from lakes Mastigou (7.6%) and des Iles (8.3%).

The larger size at maturity in white sucker females following mass removal may seem contradictory. However, because of their increased growth rate, individuals were larger at the time of reproduction. The decrease in mean age at maturity in white sucker males of Lake Rimouski after mass removal is consistent with their growth increase and would be the result of a decreased time required to reach the minimum size for reproduction. Sexual maturity is in fact more related to the attainment of a given size rather than the age (Tallman et al. 1996). Other authors also found that high growth rate is associated with decreased age at maturity (Roff 1984; Duponchelle and Panfili 1998; Rochet 1998). The decrease in age at maturity of male and female brook trout in Lake Mastigou is consistent with their growth increase. Increases in mean length at maturity observed in Lake des Iles could be explained by the larger proportion of older individuals in our sample after mass removal.

In conclusion, the present study indicates that white sucker and brook trout exhibit compensatory responses in recruitment (increase of 1+ brook trout), growth, fecundity, and length (white sucker) and age at maturity following a reduction of intra- and inter-specific competition. For all these variables, the responses were consistent with the effect as well as the intensity of mass removal. The effect of mass removal on CPUE and BPUE of white sucker, estimated by gillnet fishing before and after the biomanipulation, was significant in only one lake. However, the biomass of white sucker removed with trap nets on their spawning grounds decreased significantly 3 years after the biomanipulation in all lakes. This latter result supports that mass removal, although not of the same intensity, was important in all lakes. Given the variability of each variable, it is possible that the power of statistical analyses was lower for CPUE and BPUE of white sucker than for the other response variables. In this context, significant differences observed in abundance of 1+ brook trout as well as in growth, length and age at maturity, and fecundity of white sucker and brook trout in some lakes may be attributable to white sucker mass removal, even though no significant effects of mass removal were observed on CPUE and BPUE of white sucker in these lakes.

Our results, obtained on a gradient of mass removal intensity, support the conclusion that the success or failure of biomanipulation depends essentially on the intensity of mass removal (Colby et al. 1987; Meronek et al. 1996; Hansson et al. 1998). Our results also show that white sucker may exhibit different responses in life-history parameters through the impact of growth. Our results also suggest that white sucker is more opportunist than brook trout following a competitive release with regard to growth, reproductive investment, and time required to improve recruitment. These factors will have to be considered in future use of white sucker mass removal to improve the brook trout sport fishery.

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Calcium declines in northeastern Ontario lakes

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Abstract: Thousands of lakes in northeastern Ontario, Canada, have been acidified by sulphur deposition associated with emissions from the Sudbury area metal smelters. However, water quality improvements including increased pH and reduced sulphate concentrations have followed large reductions in Sudbury emissions that were implemented, beginning in the 1970s. Substantial decreases in Ca concentrations accompanied these other changes in lakewater chemistry. Monitoring of 38 lakes 20–128 km from Sudbury showed declines in Ca concentrations, averaging 2.7 $\mu eq \cdot L^{-1} \cdot year^{-1}$, over the period 1981–1999. Declines were particularly apparent during the 1990s, averaging 3.8 $\mu eq \cdot L^{-1} \cdot year^{-1}$. Paleolimnological reconstructions of the long-term Ca patterns in six lakes suggest that general lakewater Ca declines occurred through much of the 20th century. Comparison of recent measured Ca concentrations in 16 lakes with diatom-inferred pre-industrial Ca concentrations indicates that overall decreases in Ca have been large, averaging 74.6 $\mu eq \cdot L^{-1}$ or 46%. Long-term Ca patterns may reflect a combination of factors including climatic changes, forest harvesting activities, and leaching by acid deposition, the effects of which we can not separate. Calcium declines have biological implications that will need to be considered in the development of appropriate targets as these lakes continue to recover from acidification.

Résumé : Des milliers de lacs du nord-est de l'Ontario, Canada, ont été acidifiés par les dépôts de soufre provenant des émissions des fonderies de la région de Sudbury. Cependant, les réductions importantes des émissions depuis les années 1970 ont entraîné une amélioration de la qualité de l'eau et, en particulier, un accroissement du pH et une diminution des concentrations de sulfates. Des réductions importantes des concentrations de Ca ont accompagné ces changements dans la chimie des eaux des lacs. Le suivi de 28 lacs situés à des distances de 20 à 128 km de Sudbury indique des déclins dans les concentrations de Ca d'en moyenne 2,7 $\mu eq \cdot L^{-1} \cdot année^{-1}$ de 1981 à 1999, particulièrement durant les années 1990 où les taux étaient en moyenne de 3,8 $\mu eq \cdot L^{-1} \cdot année^{-1}$. Des reconstitutions paléolimnologiques de l'évolution à long terme du Ca dans six des lacs laissent croire que le déclin général du Ca^{2} dans l'eau des lacs s'est poursuivi pendant presque tout le vingtième siècle. Une comparaison des concentrations récentes de Ca dans 16 lacs avec les concentrations estimées d'après les peuplements de diatomées avant l'ère industrielle montre que le déclin de Ca a été important, en moyenne de l'ordre de 74,6 $\mu eq \cdot L^{-1}$ ou de 46%. Cette évolution à long terme du Ca peut être le reflet d'une combinaison de facteurs, dont les effets ne peuvent être séparés, en particulier les changements climatiques, les activités de coupe des forêts et le lessivage dû aux précipitations acides. Les déclins du Ca ont des implications biologiques qu'il sera nécessaire de considérer dans la définition d'objectifs appropriés, à mesure que ces lacs se rétablissent de l'acidification.

[Traduit par la Rédaction]

Introduction

In response to decreases in atmospheric deposition of sulphur, lakes in some areas of the world are now beginning to show signs of chemical recovery from acidification, including decreased sulphate concentrations and decreased acidity (Skjelkvale et al. 1998; Stoddard et al. 1999). However, in many regions, a large part of the declines in lakewater sulphate that have resulted from reduced sulphur deposition has been balanced by decreased concentrations of base cations, with the result that there has been little change in pH or alkalinity (Driscoll et al. 1995; Stoddard et al. 1999). Reduced export from watersheds and declines in atmospheric deposition have been implicated in the observed decreases in base cations in lake waters (Hedin et al. 1987; Likens et al. 1996). Declining concentrations of base cations, particularly Ca, may have important implications for the biological as well as the chemical recovery of acidified lakes. If the chemical recovery of acidified lakes leads to Ca concentrations that are substantially lower than historical conditions, habitat quality for aquatic biota could be affected.

Metal mining and smelting activities began around Sudbury, in northeastern Ontario, Canada, in the late 1800s. Ultimately, thousands of lakes in a large area surrounding the metal smelters near Sudbury were acidified by sulphur deposition associated with the smelter emissions (Neary et al. 1990). However, with the substantial reductions in emissions (Fig. 1) at Sudbury area smelters (over 90% since peak years in the 1960s), that began in the 1970s, considerable chemical

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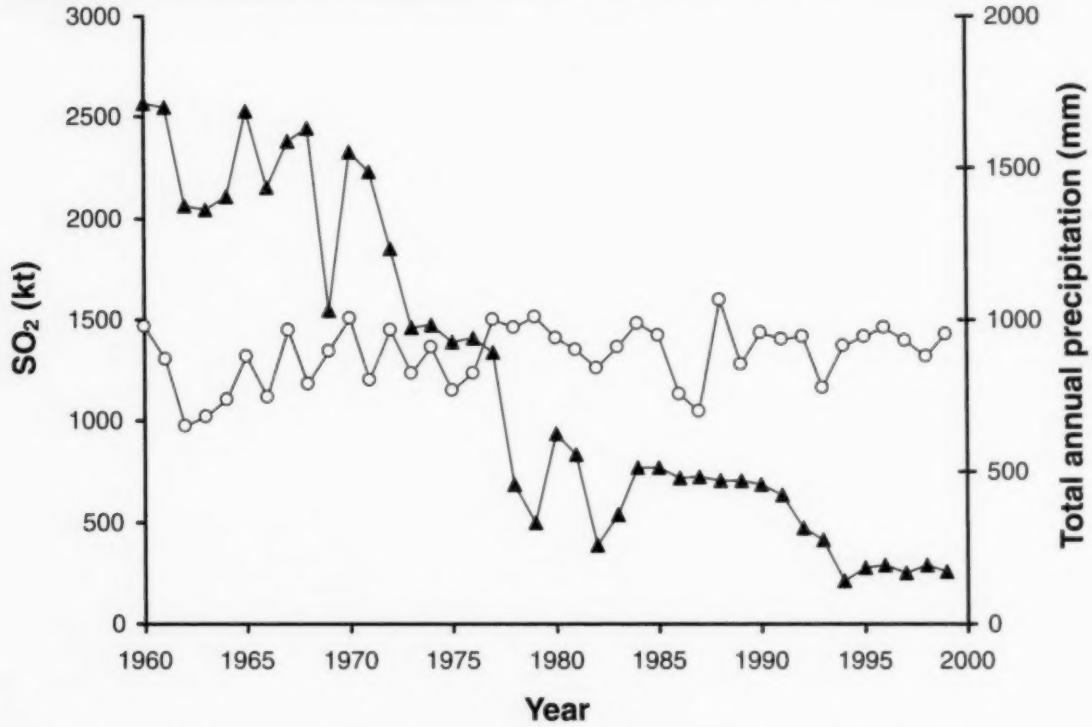
Fig. 1. Total annual precipitation (○) and sulphur dioxide emissions (▲) from the Sudbury area smelters.



and biological recovery has occurred in Sudbury area lakes (Keller 1992). At a time when evidence of chemical recovery is only beginning to emerge from lakes in other acidified regions, results from lake monitoring programs in the Sudbury area provide a unique opportunity to examine long-term patterns in lakewater Ca concentrations in acid-damaged lakes in which substantial recovery has occurred over several decades. We are rarely in a position to know what actual pre-acidification Ca concentrations were in acid-damaged areas, such as around Sudbury and elsewhere. However, paleolimnological techniques provide the opportunity to reconstruct the past in damaged lakes, and infer the magnitude of the changes in chemistry that have occurred (Smol 1995). A diatom-based Ca inference model is now available for the Sudbury region (Dixit et al. 2002). By coupling paleolimnological inferences of background Ca concentrations with measurements from ongoing monitoring studies we are able to estimate the extent of the changes in Ca that have occurred during the acidification and recovery of Sudbury area lakes.

The specific objectives of this paper are to (1) determine trends in measured Ca concentrations in 38 Sudbury area lakes over the last two decades; (2) reconstruct, using a diatom-based Ca inference model, the long-term temporal patterns in Ca in six Sudbury area lakes that are recovering from acidification; (3) estimate overall changes by comparing recent Ca concentrations to inferred pre-industrial conditions in 16 of our monitoring lakes for which paleolimnological analyses have been conducted; and (4) discuss the factors potentially responsible for Ca declines. Our overall goal is to evaluate the changes in Ca that have occurred in Sudbury area lakes and examine the implications of these changes for the lake recovery process and aquatic biota.

Methods

Chemical monitoring

The measured Ca data examined in this paper are from synoptic (single annual mid-summer samples) surveys of 38 lakes (Fig. 2) 20–128 km from Sudbury, which have been sampled since 1981. The lakes are in various stages of recovery from acidification. When monitoring began in 1981 the pH of these lakes ranged from 4.3 to 5.8. In 1999 lakewater pH ranged from 4.6 to 6.7. A summary of general chemical and physical characteristics of the lakes is provided in Table 1. These lakes are a subset of a slightly larger lake set ($n = 44$) that is regularly sampled (Keller et al. 1998). For this analysis, however, we excluded lakes that are located within 20 km of Sudbury in which urban influences might complicate the interpretation of Ca trends. Calcium data are available for most lakes for every year from 1981 to 1999, but some lakes are missing data for some years.

Sampling methods and general descriptions of the lakes are given in Keller and Pitblado (1986) and Keller et al. (1998). Briefly, mid-lake chemistry samples were collected at surface or as non-volume-weighted epilimnion–metalimnion composites, which are comparable in these lakes (Keller and Pitblado 1986). Water samples were analysed for Ca by atomic absorption spectrophotometry at the Ontario Ministry of the Environment laboratories in Toronto (Keller et al. 1998).

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Fig. 2. The zone of lakes influenced by the Sudbury smelters, defined by the extent to which sulphate has replaced bicarbonate (sulphate/[sulphate + alkalinity] > 0.7) as the dominant anion in lake waters. This 17 000 km^2 zone contains over 7000 lakes estimated to have been acidified to pH < 6.0, the apparent threshold for significant biological damage (Neary et al. 1990). ●, locations of the 38 monitoring lakes; ○, locations of the six lakes with downcore profiles shown in Fig. 6 (AD, Acid; AWP, Aurora Whitepine; GE, George; LWP, Little Whitepine; LN, Lumsden; WPM, Whitepine McLeod). ■, locations of major current (Cc, Copper Cliff; Fa, Falconbridge) and historical (Co, Coniston) smelter sites.

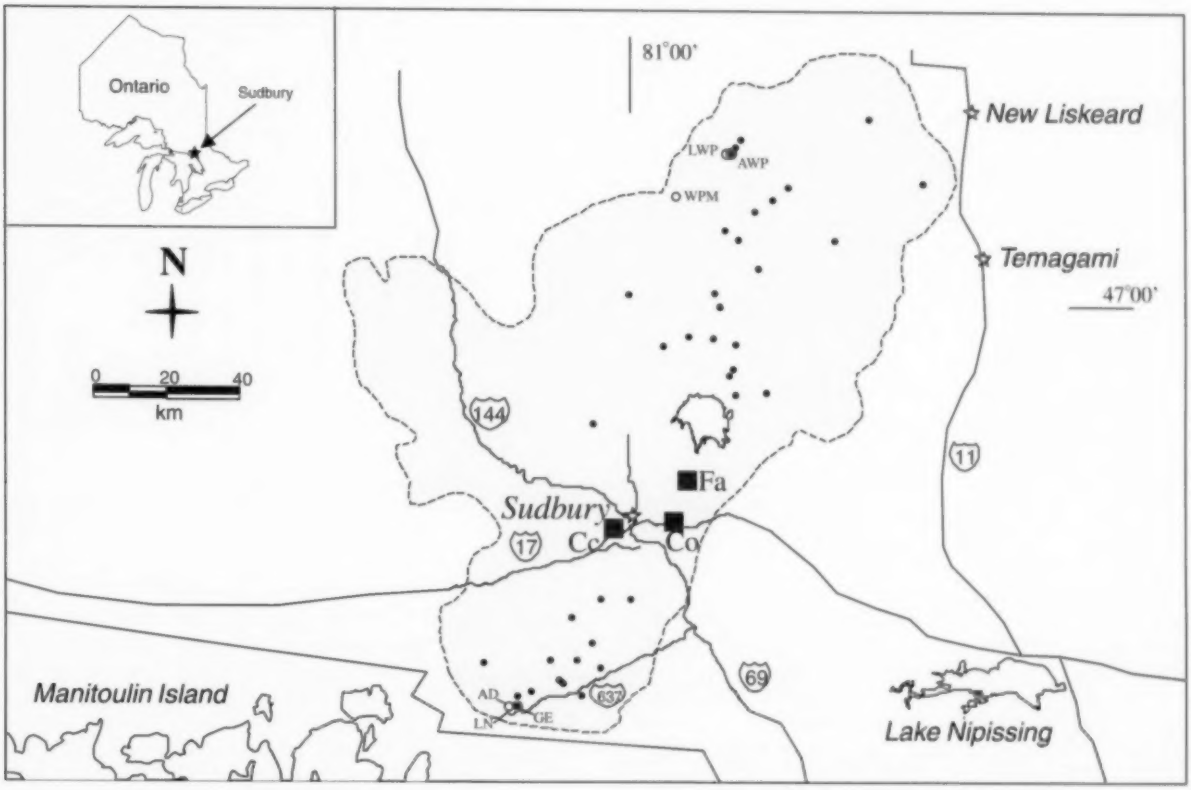

Table 1. General physicochemical characteristics of the 38 monitoring lakes.

Parameter	Mean	Median	Min.	Max.	*n*
Area (Ha)	295.3	192.5	14.5	1315.5	38
Mean depth (m)	9.8	8.0	4.1	24.1	34
Maximum depth (m)	33.5	32.9	11.0	90.3	35
pH	5.3	5.6	4.6	6.7	38
Conductivity ($\mu S \cdot cm^{-1}$)	26.9	27.1	20.2	34.3	38
Total phosphorus ($\mu g \cdot L^{-1}$)	3.9	4.0	2.0	16.0	38
Total nitrogen ($\mu g \cdot L^{-1}$)	150.0	150.0	40.0	360.0	38
Dissolved organic carbon ($mg \cdot L^{-1}$)	2.2	2.3	0.1	6.6	38

Note: Chemistry data are from 1999. Min., minimum; Max., maximum.

Paleolimnology

Details of paleolimnological methods, including sediment core collection, preparation of diatom slides, and analysis of diatoms are presented in Dixit et al. (1991, 2002). The WACALIB (version 3.3) program (Line et al. 1994) was used for developing a weighted-averaging (WA) regression and calibration model for Ca (for details see Dixit et al. 2002). Our model included the surface sediment diatom assemblages from 105 Sudbury area lakes. To reconstruct past Ca concentrations, we applied our Ca inference model to downcore samples from six Sudbury area lakes and the bottom sediment samples (representing pre-industrial conditions) from 16 lakes. The detailed diatom stratigraphy of the six lakes considered in this study and their pH reconstructions are presented in Dixit et al. (1992*a*, 1993, 1996). For the use of bottom sediments in assessing post-industrial water quality changes in Sudbury lakes see Dixit et al. (1992*b*).

Results

Trends in measured calcium, 1981–1999

Calcium concentrations in 23 of our 38 monitoring lakes that

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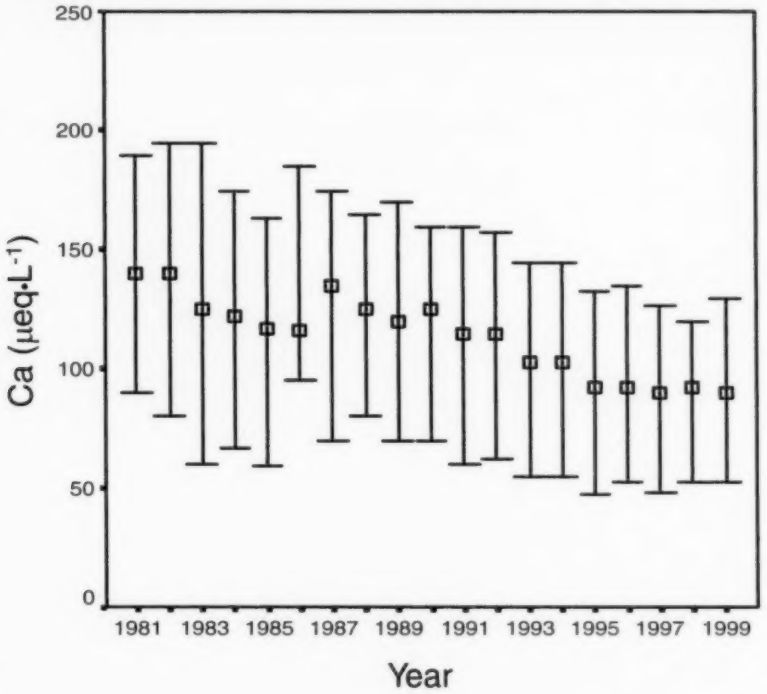
Fig. 3. Annual median and range for Ca concentrations in 23 of the monitoring lakes with data from 1981 to 1999.



have data for all years (Fig. 3) ranged from 89.8 to 189.6 $\mu eq \cdot L^{-1}$ in 1981 (mean, 136.2; median, 139.7) and 52.4 to 129.7 $\mu eq \cdot L^{-1}$ in 1999 (mean, 86.1; median, 89.8).

Linear regression analyses of measured Ca concentration against year of sampling showed significant ($p < 0.05$) declines in all 38 of the lakes during the overall continuous monitoring period of 1981–1999 (n = 17–19), and during 1990–1999 (n = 9–10). Average rates of decline were 2.7 $\mu eq \cdot L^{-1} \cdot year^{-1}$ and 3.8 $\mu eq \cdot L^{-1} \cdot year^{-1}$ during 1981–1999 and 1990–1999, respectively. Significant ($p < 0.05$) linear declines in Ca concentrations were found in only 15 (39%) of the study lakes during 1981–1989 (n = 7–9), although all but two of the lakes did in fact decrease in Ca over this period, and on average Ca declined by 1.9 $\mu eq \cdot L^{-1} \cdot year^{-1}$. Exploratory analyses examining nonlinear relationships (logarithmic, inverse, exponential) between Ca and sampling year for the above study periods did not improve our ability to explain temporal patterns. The magnitude of the Ca declines during the 1990s showed a strong relationship to distance from the Sudbury smelters (Fig. 4).

The calcium inference model

Statistical details considered in evaluating the significance of environmental variables in determining the distribution of diatom assemblages in surface sediments of the 105 Sudbury calibration lakes are presented in Dixit et al. (2002). Here we summarize details pertaining to Ca data. Canonical correspondence analysis (CCA) identified seven significant ($p < 0.01$) environmental variables (pH, Al, Ca, Secchi depth, Ni, Fe, and elevation) in the 105-lake calibration data set, explaining 77% of the total diatom species variance. Among these variables, Ca explained 11% of the total variance in diatom species data and only ranked after pH (31%) and Al (12%). Constrained and partial CCAs and Monte Carlo permutation tests further confirmed the significance ($p < 0.005$) of Ca in our data set. High λ_1/λ_2 values for Ca in constrained (0.65) and partial (0.39) CCAs provided strong evidence that Ca is one of the most important variables in explaining the distribution of diatoms in Sudbury lakes and that a robust diatom-based inference model can be developed for inferring lakewater Ca.

The WA regression and calibration approach (classical regression without tolerance downweighting) was used for developing the diatom-inferred Ca model. The WA approach is widely used in paleolimnological research for the quantitative reconstruction of past environmental conditions (Birks 1998). The relationship between measured and inferred Ca indicates that the simple WA model (Fig. 5*a*) has a high correlation ($r^2 = 0.72$) and low apparent root mean square error (RMSE) (0.32), and the residuals (plot of measured minus inferred Ca and measured Ca) do not show any pattern (Fig. 5*b*). In comparison to simple WA, the WA bootstrap model for Ca (Fig. 5*c*) has a lower correlation ($r^2 = 0.58$) and higher bootstrap RMSE (0.35). Because bootstrap models provide more realistic assessments of the strength of inference models (Birks 1998), this model was used for computing downcore Ca inferences in this study. Bootstrapping is a computer-intensive resampling procedure where a subset of calibration samples that is the same size as the original calibration set is selected at random, with replacement, and the remaining unselected samples form an independent test set. A trend in the residuals of the bootstrap

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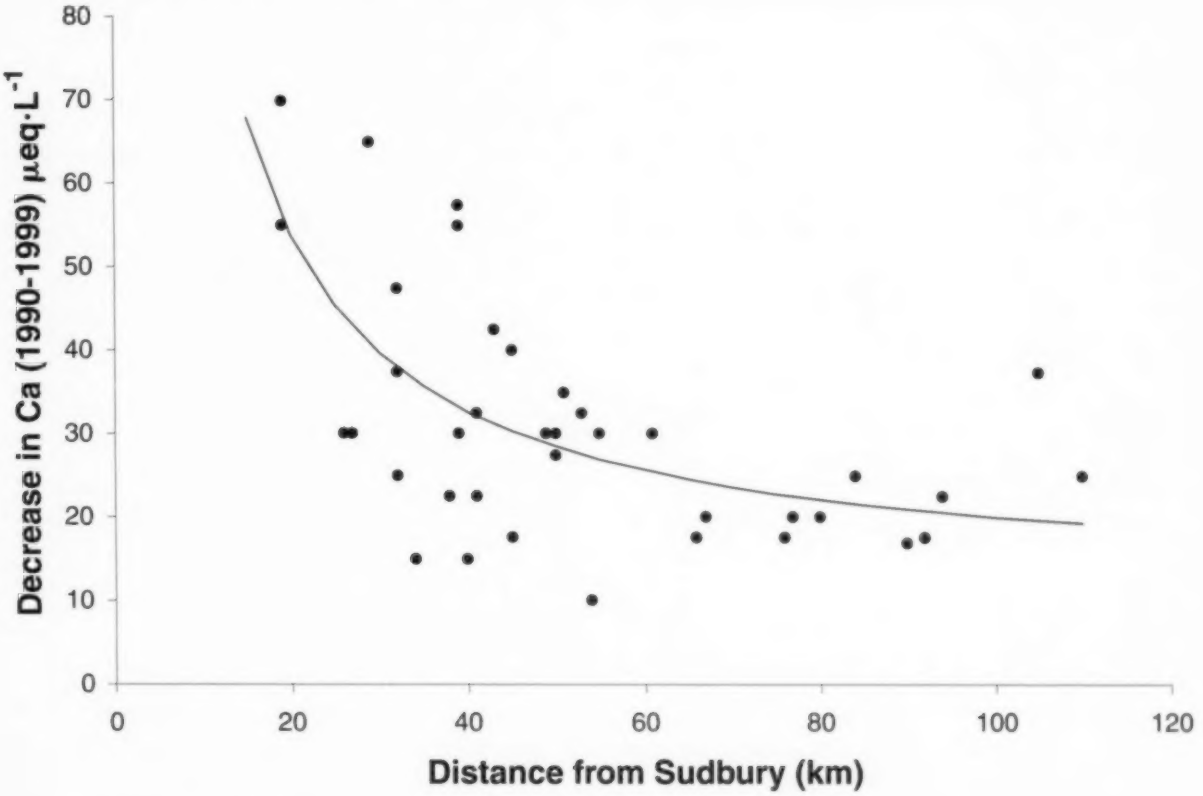
Fig. 4. Decrease in Ca in Sudbury area lakes between 1990 and 1999 as a function of distance from Sudbury ($y = 11.6010 + (843.534/x)$, $n = 38$, $F = 22.27$, $r^2 = 0.382$, $p < 0.001$).



model (Fig. 5*d*) suggests that our Ca model likely underestimates inferred Ca at higher concentrations. Although we recognize that the statistics of our Ca model are not as strong as the bootstrap pH model ($r^2 = 0.79$) for Sudbury lakes (Dixit et al. 2002), our Ca inferences are useful for assessing the past trends in lakewater Ca concentrations in Sudbury area lakes. There was a good correlation ($r^2 = 0.43$, $p < 0.05$, $n = 16$) between inferred downcore Ca and measured Ca, in the four of the lakes with detailed core profiles (Aurora Whitepine, George, Little Whitepine, Whitepine McLeod) for which there was some temporal overlap in measured and inferred values. Average Ca values for these downcore inferences and measurements (2.31 mg·L^{-1} and 2.22 mg·L^{-1}, respectively) were not significantly different ($p > 0.05$, $n = 16$) based on a paired t test.

Long-term changes in calcium

In the six lakes for which detailed profiles were examined, inferred temporal patterns showed substantial variation between lakes over the period covered by our sediment cores, from the mid-1800s to the late 1980s (Fig. 6). Lake-specific factors such as differences in catchment soils and forest cover may account for this variability. However, with the exception of Aurora Whitepine Lake, which showed little change in inferred Ca, the lakes showed substantial declines in Ca beginning in the early to mid-1900s (Fig. 6). While our inferences do describe the long-term Ca trends in these lakes, they do not appear to be sensitive enough to effectively capture shorter-term variations in Ca that likely occurred, such as the elevated concentrations reported in the early to mid-1970s in many Sudbury area lakes (Conroy et al. 1978) following the period of maximum smelter emissions.

Overall changes in Ca concentrations in Sudbury area lakes have been substantial. For the 16 of our 38 monitoring lakes for which we have pre-industrial Ca inferences, the estimated decreases ranged from 27.2 to 133.0 µeq·L^{-1} (26.4–64.0%) and have averaged 74.6 µeq·L^{-1} (46%) based on a comparison of pre-industrial inferences and recent (1999) measurements (Fig. 7).

Discussion

Water quality improvements, including increases in pH and decreases in sulphate concentrations, have followed the large reductions in Sudbury area sulphur emissions (Keller et al. 1992). These improvements have been accompanied by substantial decreases in Ca concentrations, averaging 2.7 µeq·L^{-1}·year^{-1} over the 1980s and 1990s. During our two-decade monitoring period, declining trends in Ca concentrations, averaging 3.8 µeq·L^{-1}·year^{-1}, were universal during the 1990s. Assessment of trends in Ca during the 1980s is complicated by the effects of a two-

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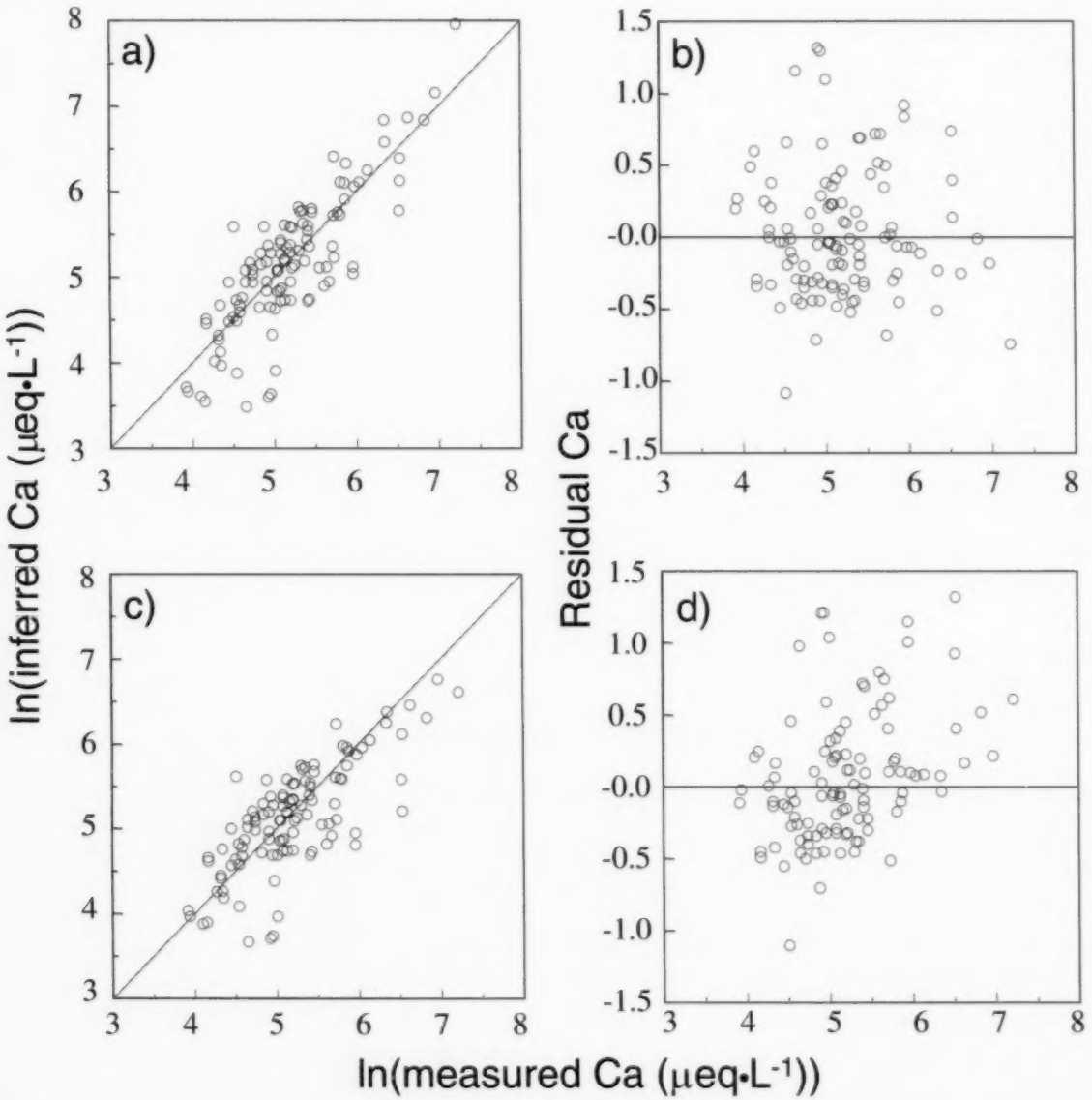
Fig. 5. Diatom-based inference models for lakewater Ca. The relationships between ln measured and diatom-inferred Ca and residuals for simple weighted averaging (*a* and *b*) and bootstrap weighted averaging (*c* and *d*) are shown. (*a*) $r^2 = 0.72$, RMSE = 0.32; (*b*) $r^2 = 0.00$; (*c*) $r^2 = 0.58$, $RMSE_{boot} = 0.35$; (*d*) $r^2 = 0.21$.



year (1986–1987) drought followed by abundant precipitation, which caused short-term Ca increases and other water quality changes in some Sudbury area lakes in the late 1980s (Keller et al. 1992; Yan et al. 1996). Nevertheless, almost all of our lakes showed overall Ca declines during the 1980s, although less than half (39%) showed significant trends. The average rate of decline of 1.9 $\mu eq \cdot L^{-1} \cdot year^{-1}$ in our study lakes during the 1980s is substantially higher than rates of 0.6–1.3 $\mu eq \cdot L^{-1} \cdot year^{-1}$ reported by Driscoll et al. (1995) for seven Adirondack lakes that showed significant declines in Ca during the 1980s.

The positive relationship between Ca declines in the 1990s and increasing proximity to Sudbury indicates a continuing "Sudbury" effect on lake chemistry, even though we have excluded the lakes closest (<20 km) to Sudbury from this analysis. However, this effect is only apparent in lakes relatively close to the smelters, within about 45 km, as has been previously observed for lakewater sulphate concentrations (Keller et al. 2001). Much of this effect may be historical, and not related to current smelter emissions. The additional sulphur emission controls that were implemented at the Sudbury smelters during the 1990s may be contributing to continuing lake recovery (Keller et al. 1999). How-

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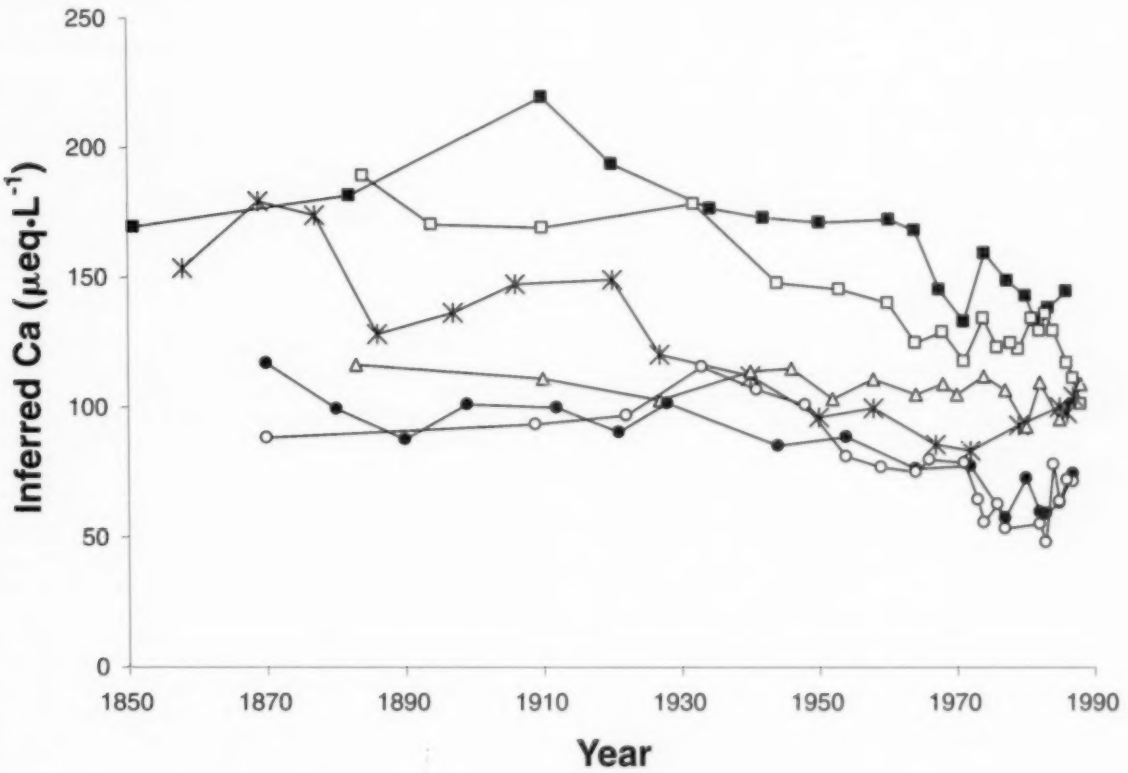
Fig. 6. Downcore diatom-inferred Ca trends for six study lakes. Acid (●), George (✳), and Lumsden (○) lakes are 60–62 km southwest of Sudbury; Aurora Whitepine (△), Little Whitepine (□), and Whitepine MacLeod (■) lakes are 88–102 km northeast of Sudbury (see Fig. 2).



ever, evidence suggests that Ca declines in the 1990s were not primarily due to recent changes in acid deposition and associated Ca leaching attributable to the Sudbury smelters. Studies in 1978–1980 indicated that the Sudbury emissions were no longer a major contributor to sulphur deposition in the Sudbury area, constituting about 25% or less (Chan et al. 1984). The current Sudbury contribution to regional sulphur deposition is expected to be even lower, with the additional emission reductions that were implemented in the 1990s. Recent (1990s) decreases in Ca in lakes near Sudbury are correlated with declines in sulphate ($r^2 = 0.53$, $p < 0.01$), and may be a continuation of the long-term recovery of lakes and watersheds around Sudbury that began decades ago (Keller 1992) and may also still be reflecting recovery from the drought-induced re-acidification event in the 1980s (Keller et al. 1992; Yan et al. 1996).

Our observation that the 1990s Ca declines in lakes further than about 45 km from Sudbury were not related to distance suggests that since the Sudbury smelter emissions have been greatly reduced, base cation changes in Sudbury lakes more distant from the smelters may now be affected primarily by broad patterns of continental long-range transport and atmospheric deposition. Generally, similar patterns of a strong decline during the 1990s were also observed for base cations in the surface waters of other areas of North America, including south-central Ontario, and the Adirondack and Catskill mountains of the U.S.A. (Stoddard et al. 1999). While the large local sources of sulphur emissions clearly dominated the acidification process in Sudbury area lakes (Keller 1992), it appears that the recovery process in many of these lakes will now be more linked to the effects of long-range atmospheric transport.

Comparison of recent lakewater Ca concentrations in Sudbury area lakes and paleolimnological inferences of pre-industrial conditions indicates that substantial overall declines in Ca concentrations, averaging 46%, have occurred. The general patterns of decline in Ca observed over the latter half of the 20th century in our lakes are consistent with the hypotheses that (1) base cations in lake catchments were gradually depleted as a result of acid deposition, and (2) that leaching rates of easily exchangeable Ca have then declined as acid deposition decreased owing to sulphur emission controls in the Sudbury area and elsewhere. However, other factors including climate variations, forest harvesting, and reduced Ca deposition from the atmosphere may also have substantially influenced the Ca concentrations in these lakes over the long term. The same general pattern of Ca decline has been observed for waters in other regions, notably streams in the Hubbard Brook Experimental Forest in New Hampshire, and has been attributed to a combination of leaching by acid deposition, decreased Ca inputs from the atmosphere, and changing net Ca storage in biomass (Likens

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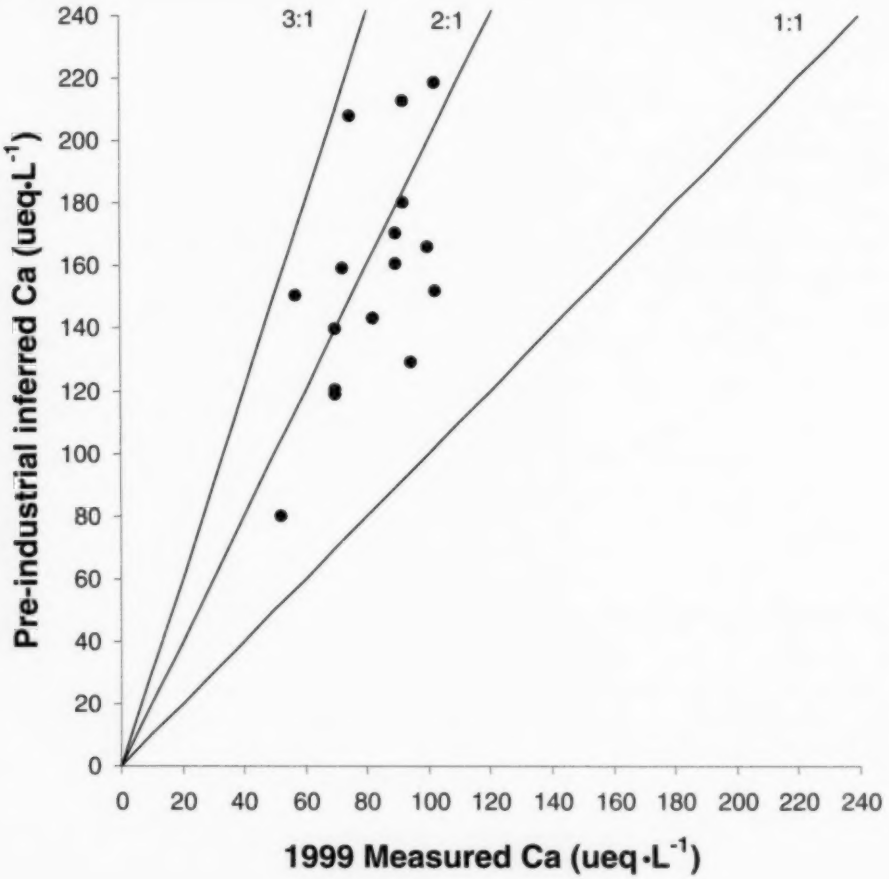
Fig. 7. Plot of pre-industrial inferences vs. recent (1999) measured Ca for 16 monitoring lakes. Lines representing 1:1, 2:1, and 3:1 relationships are shown.



et al. 1998). Changes in climate can also affect temporal patterns of Ca in lakes (Schindler et al. 1990; Sommaruga-Wograth et al. 1997).

While we cannot currently evaluate the relative roles of the different factors potentially affecting Ca concentrations in our lakes, the net effect has been a substantial decline in lakewater Ca concentrations. This may have important biological implications for these lakes as they continue to recover from acidification. Calcium is known to ameliorate the toxicity of acid and metals to fish, thus concern has been expressed that in some cases, declines in Ca during lake recovery may offset some of the biological benefits of modest acidity decreases (Skeffington and Brown 1992). It has recently been demonstrated that the sensitivity of *Daphnia* to UV radiation increases at low Ca concentrations (Hessen and Alstad Rukke 2000). Calcium may also have other, direct effects on biota since Ca is an essential element for aquatic species with a calcified exoskeleton, including some crustacean zooplankton (Alstad et al. 1999). Calcium availability may influence competitive interactions between some zooplankton species and influence species distributions (Hessen et al. 1995; Alstad et al. 1999).

Tessier and Horowitz (1990) demonstrated that substantial changes in zooplankton community size structure, largely attributable to losses of large-bodied *Daphnia* at lower Ca levels, occurred along a gradient of Ca concentrations. Thresholds for changes in zooplankton communities appeared to occur between 200 $\mu eq \cdot L^{-1}$ and 300 $\mu eq \cdot L^{-1}$ and at about 50 $\mu eq \cdot L^{-1}$. There is also evidence for increased sensitivity of fish to H^+ and Al at Ca levels below about 50 $\mu eq \cdot L^{-1}$ (Brown 1983). Based on our sample, most acidified lakes in our study area likely never had Ca concentrations over 200 $\mu eq \cdot L^{-1}$ before industrialization. While they are not as Ca poor as some acidified lakes in other affected regions such as Norway (Skjelkvale et al. 1998) or the Adirondack Mountains of New York (Driscoll and Van Dreason 1993), some of our study lakes are nonetheless approaching 50 $\mu eq \cdot L^{-1}$. For crustacean zooplankton and other invertebrates that have relatively high Ca requirements, Ca limitation may become an important influence if decreases continue. Calcium limitations on invertebrates could also have nutritional effects on other components of food webs. The potential effects on aquatic birds of reduced availability of Ca from prey in acidic lakes are already of concern (McNicol 1999). Calcium concentrations in Sudbury area lakes, and in lakes of other acid-affected re-

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gions will need to be closely monitored. Ca declines may be an important factor to consider in the development of realistic biological targets for lakes recovering from acidification.

Acknowledgements

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The role of coastal ocean variation in spatial and temporal patterns in survival and size of coho salmon (*Oncorhynchus kisutch*)

Alistair J. Hobday and George W. Boehlert

Abstract: Interannual and decadal variability in ocean survival of salmon are well known, but the mechanisms through which environmental variability exerts its effects are poorly understood. Data on hatchery-reared coho salmon (*Oncorhynchus kisutch*) from individual releases (1973–1998) along the species' entire North American range were analyzed to provide information on survival and size. Three geographic regions (north of Vancouver Island, Puget Sound and Strait of Georgia, and the outer coast south of the tip of Vancouver Island) showed coherent trends in survival and size of returning fish. Within each region, multivariate nonlinear models were used to relate coho survival and final size to spatially and temporally tailored environmental variables at time periods of release, jack return, and adult return. The most important environmental variable, as indicated by the highest amount of variance explained, was a calculated proxy for mixed-layer depth, followed by sea level. In all regions, survival and adult size were most influenced by environmental conditions at the release time. A shallow mixed layer was associated with increased survival and decreased size in all regions. Improved understanding of the relationship between environmental conditions and size and survival of coho salmon provides insight into production patterns in the coastal ocean.

Résumé : La variation d'une année à l'autre et d'une décennie à l'autre de la survie des saumons en mer est un phénomène bien connu, bien que les mécanismes par lesquels la variabilité de l'environnement peut agir restent mal compris. L'analyse de données provenant d'empoissonnements individuels (1973–1998) de Saumons cohos (*Onchorhynchus kisutch*) de pisciculture sur toute l'étendue de la répartition géographique de l'espèce en Amérique du Nord a fourni des renseignements sur la survie et la taille. Trois régions géographiques (le nord de l'île de Vancouver, Puget Sound et le détroit de Géorgie, ainsi que la côte extérieure au sud de l'extrémité de l'île de Vancouver) affichent des tendances cohérentes dans la survie et la taille des poissons qui rentrent de la mer. Dans chaque région, des modèles multidimensionnels non-linéaires ont permis de relier la survie et la taille terminale des saumons aux variables de l'environnement correspondant, dans le temps et l'espace, aux périodes d'empoissonnement, de retour des saumoneaux et de retour des adultes. Les variables de l'environnement les plus importantes, qui expliquent le maximum de variance, sont d'abord une valeur indirecte calculée de la profondeur de la couche mixte, puis le niveau de la mer. Dans toutes les régions, la survie et la taille des adultes sont affectées surtout par les conditions de l'environnement au moment de l'empoissonnement. Une couche mixte de faible profondeur est associée à une augmentation de la survie et à une diminution de la taille dans toutes les régions. Une meilleure compréhension des relations entre les conditions de l'environnement et la taille et la survie des Saumons cohos permet une connaissance des patterns de production dans l'océan côtier.

[Traduit par la Rédaction]

Introduction

Environmental variability affects production in fish stocks, often in predictable ways and often with greatest impact on early life-history stages (Houde 1997). The relationships can become more complex for species inhabiting or migrating through a broad geographic range; the diversity of environmental factors impacting survival may vary with location or with life-history stage. For species with a high level of "population richness", localized and often self-sustaining populations may have larval and older life stages retained in areas that are characterized by different environmental features (Sinclair and Iles 1988); thus, survival and growth among populations may respond to different types of physical forcing. Recognizing the scale of physical forcing remains a goal for fisheries oceanography.

Production of marine fish like salmon is influenced by three processes: survival, age at maturity, and size (growth) (Peterman et al. 1998; Pyper et al. 1999). Variability in these components is well documented on a range of spatial and temporal scales (Steele 1996). At the ocean basin scale, correlations exist between atmospheric and oceanographic indices (i.e., the Aleutian Low Pressure Index, North Pacific Index, Pacific Decadal Oscillation, and Southern Oscillation

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Index) and time series of catch of North Pacific salmon stocks (e.g., Mantua et al. 1997), but the actual combination of physical and biological processes that determines these linkages has not been identified (Beamish et al. 2000). These higher-order processes are assumed to influence the environment by acting on the "primary" environmental variables (e.g., temperature) at the local scale; for Atlantic salmon, spatial coherence of marine survival suggests that broad-scale forcing functions play an important role (Friedland et al. 2000). At the species level, relationships exist between regional survival and single environmental variables (Nickelson 1986; Cole 2000) or linear combinations of the variables (Koslow et al. 2001), but it has been difficult to discern the mechanisms involved. Fewer studies have explored how environmental variables affect salmon size and survival at even finer temporal and spatial scales that affect individual stocks or river systems (Coronado and Hilborn 1998; Ryding and Skalski 1999). The broad latitudinal ranges of many salmon species subject the young stages to different ocean conditions, and some populations also inhabit different ocean areas in the adult stages (Myers et al. 1996). Indeed for some species, long-term inverse patterns of production have been observed between the northern and southern ends of their geographic range (Hare et al. 1999). Although long-term variation in salmon survival and size may be linked to large-scale climatic variation (Ricker 1995; Pyper et al. 1999), it is the shorter-scale variation that is explored here.

Environmental variation also impacts management of economically important marine fisheries like salmon. Unfortunately, management decisions are based largely on predictions from historical stock size and population production characteristics that typically give inadequate weight to variability in environmental conditions. Changes in ocean conditions do affect salmon stocks and disrupt predictions based on population size alone (Francis and Hare 1994; Peterman et al. 1998) and may leave populations vulnerable to overfishing and collapse. Correlation-based analyses of stock dynamics that include environmental data have provided important inferences to guide research, but an understanding of mechanistic relationships is needed to provide better overall predictions as part of management and recovery strategies (Tyler 1992). Examination of environmental factors that may influence production in the nearshore ocean should be a priority for research on the ocean phase of salmon life (Brodeur et al. 2000). Understanding the role of variation in the nearshore ocean with salmon survival will lead to more efficient management, including matching of expensive artificial production to the carrying capacity of the nearshore ocean, replenishment of natural stocks, and setting appropriate escapement for salmon fisheries (Bradford et al. 2000; Welch et al. 2000).

The belief that nearshore ocean dynamics are important influences on salmon survival (Pearcy 1992; Gargett 1997) is supported by (*i*) correlation between salmon survival and various nearshore environmental variables (e.g., Nickelson 1986); (*ii*) coherence in survival of stocks in the same region (Beamish et al. 1997; Peterman et al. 1998); and (*iii*) common survival patterns in the same year for different year classes (Pearcy 1992; Weitkamp et al. 1995). Furthermore, many of these previous studies suggest that most variance in survival occurs in the first 6 months of ocean life; however, the influence of the environment at the time when salmon return to spawn has rarely been considered. Mechanisms through which environmental variability affects salmon survival and size include principally predation, starvation, and impacts on growth rate (Pearcy 1992). However, the nature of most of these linkages is speculative because of the lack of adequate field data.

Coho salmon (*Oncorhynchus kisutch*) have a broad geographic range along the west coast of North America, appear to be particularly sensitive to environmental conditions, and have a relatively simple 3-year life cycle (Sandercock 1991; Pearcy 1992). They are thus suitable for the exploration of relationships between nearshore ocean conditions and two of the components of production, survival and size. Wild juveniles remain in freshwater for up to 15 months and then migrate to the ocean as smolts. Despite some regional variation, most coho salmon return to spawn in their natal streams after 18 months in the ocean, with a smaller fraction of precocious males (jacks) returning after only 6 months of ocean residence (Sandercock 1991; Weitkamp et al. 1995; Coronado and Hilborn 1998).

In this paper, we first apply cluster analyses to identify the regions of the west coast of North America having coherent patterns in survival and final size of hatchery-released coho salmon, indicating common effects of the marine environment. Then, within each region, the variance in survival and final size of individual releases was evaluated with respect to environmental variability at time and space scales appropriately tailored to the release and return periods. Finally, we evaluate the most important environmental variables affecting coho survival and size in each region and speculate on mechanisms that link these variables to coho salmon.

Methods

Biological data

Survival and size data from coded wire tag (CWT) hatchery fish were used. This minimizes the variation resulting from freshwater conditions as in-river residence time is short and barriers to migration are limited or nonexistent. Restricting analyses to releases from hatcheries close to the mouth of the river may further reduce the time for the freshwater portion of the life cycle to influence survival. Patterns of survival derived from hatchery fish may match or track survival patterns of wild salmon (Koslow et al. 2001), although hatchery practices and conditions may also result in lower overall survival than for wild fish (Weitkamp et al. 1995). Some CWT are applied to wild smolts, but these data are extremely limited and would not allow extensive analyses over the desired spatial and temporal scales. Hence, this analysis is limited to using hatchery CWT data to explore the relationship between environmental conditions and salmon production.

Biological data on hatchery CWT coho salmon released between 1973 and 1998 were obtained from the Pacific States Marine Fisheries Commission Regional Mark Information Center (see Johnson (1990) for details and for how survival is calculated). Only data from age-1 nonexperimental normal releases were included in analyses. It is important to note that there have been changes in rearing practices over time and hatchery conditions are not uniform between hatcheries; however, these differences have been ignored in this large-scale analysis. Survival and "returns by year" (catch plus escapement) were summarized for each tag code and the number of jack and adult returns were determined for each release tag code by year and state. Because fewer than 1% of total coho

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returns occur after more than 2 years at sea (Weitkamp et al. 1995; Coronado and Hilborn 1998), standardizing survival to a single age at recovery was not undertaken. The average survival for each hatchery was then calculated for each year.

Individual fish final size information was also obtained from the CWT database for the same tag codes. Only records that included final length were retained for subsequent size analyses. Initial data processing consisted of converting lengths given as mid-eye fork length to the more commonly listed fork length (FL) using accepted methods (Fleming and Gross 1990). Other measurements were not common enough or had potential conversion errors and were not included. Output from preliminary treatment of the final size data was average final length, standard deviation, and number for each release tag code by year of return and by fishery. The fisheries considered were (*i*) marine troll, (*ii*) marine net and seine, (*iii*) freshwater net and seine, and (*iv*) hatchery captures. Because each fishery might target fish of different ages and sizes, data from each fishery were kept separate. Differences in final size between sexes were considered by fishery; however, sex was not provided for most records. Preliminary analyses of the limited sex data found differences in size between sexes only for some release groups captured at the hatchery. Because of these preliminary findings and limited data, sex was ignored when calculating the final average size for a release. The average size of fish by age class returning to each hatchery from each release batch was calculated for each year by hatchery for each fishery. Fish spending more than 1 adult year in the ocean were not included in subsequent size analyses owing to limited data for these age classes.

Survival was standardized for each hatchery, whereas jack size and adult size data were standardized by each hatchery and fishery combination ((value – mean)/standard deviation). Standardizing the final size of fish captured in each fishery allowed the final size data for adults and jacks to be combined into a single-size data set for each period. We did not account for changes in fishing regulations that may have influenced the size of fish captured within single fisheries (e.g., Ricker 1995), but standardization does allow data from fish captured in different fishery seasons to be combined. Data sets were created for two periods because cluster formation may be sensitive to hatcheries with limited data. The first set was from hatcheries that had more than 9 years of data for the full period (1973–1998), and the second set included hatcheries with more than 9 years of data for a shorter period of 1980–1994. This meant that all hatcheries in the second data set had at least five common years. Creating two data sets allowed a measure of quality control. If cluster results from both were similar, then the larger data set could be used in subsequent analyses.

The geographic coordinates for each hatchery that released coho are not provided in the CWT database. Hatchery locations and the ocean-entry coordinates for the river mouth on which each hatchery was located were compiled from a variety of sources (L. Weitkamp, NOAA-NMFS, 2725 Montlake Blvd. E, Seattle, WA 98112, personal communication). In this study, releases of fish were assumed to take place at or close to the hatchery location (experimental releases, where fish may have been transported to another location, were not included). Linear hatchery – ocean-entry distances were computed and used as an estimate of the distance upstream that fish were released. This subsequently allowed selection of releases made within a maximum distance from the coast, which minimized the period of time that the smolts were migrating in freshwater and hence the influence of freshwater conditions on size and survival patterns (see Solazzi et al. 1991).

Cluster analysis

Cluster analysis was undertaken to identify groups of hatcheries (i.e., geographic regions) with similar annual survival or size patterns for each data set. The standardized size and survival data were used to generate clusters using the *k*-means method (SYSTAT 5.0, SPSS Inc., Chicago, Ill.) This clustering method is nonhierarchical and the number of clusters to be found must be specified. Two to eight clusters were generated for each data set. Comparison of the geographically meaningful cluster patterns for each data set allowed regions with similar patterns of final size and survival to be identified.

In addition to identifying regions with different patterns, cluster analyses also revealed the years t in which the clusters were statistically distinct via an analysis of variance style test. Temporal trends in the standardized data for each cluster were investigated using regression analysis. In all statistical tests, significance was defined as $\alpha < 0.05$.

The releases in each region identified by the cluster analysis were processed to select portions for further analyses with respect to environmental data. Data subsets were defined to include only releases (*i*) from hatcheries less than 100 km inland from the coast, (*ii*) occurring over less than a 10-day period, and (*iii*) with more than 10 000 fish.

Environmental data

Lack of understanding about causal mechanisms that produce the observed biological variance often leads to speculative consideration of variables, guided by knowledge of the system, biology of the component parts, and data availability. Six environmental variables that might influence coho salmon survival and final size were chosen to match the temporal resolution in the individual release data. We specifically chose variables used previously in studies of recruitment in marine fish, including three derived from wind (wind speed, upwelling, and cube of wind speed), two measured parameters (sea level, sea surface temperature (SST)), and a derived index of mixed-layer depth. The coast was divided into adjacent 1° latitude × 1° longitude boxes (hereafter referred to as 1° boxes), and daily environmental averages for the period of 1970–1998 were obtained for each box (Fig. 1).

Average daily wind speed was calculated from the National Centers for Environmental Prediction (NCEP) surface wind data for each 1° box (NCEP reanalysis data were provided by the NOAA-CIRES Climate Diagnosis Center, Boulder, Colo., http://www.cdc.noaa.gov/). The daily averages were an average of six hourly data points on a 2.5° grid. East–west (u) and north–south (v) components of the wind were interpolated to the center of each 1° box before computing the wind speed. The alongshore (v-wind) component was used in analyses.

The offshore component of Ekman transport provides a proxy for upwelling (Bakun 1973). Average daily cross-shelf upwelling for the midpoint of each 1° box was calculated from the geostrophic winds derived from surface atmospheric pressure fields at Pacific Fisheries Environmental Laboratory (NOAA; data available at http://www.pfeg.noaa.gov/products/las.html).

The wind imparts energy to the ocean surface proportionally to the cube of wind speed, which is thus a potential index of turbulence. Average daily cubed wind speed ((wind speed)^3) was calculated from the wind speed for each 1° box using the NCEP data.

Sea level at the coast is often used as a measure of alongshore transport (Reid and Mantyla 1976; Strub et al. 1987). When transport to the south is high along the coast of North America, coastal sea level is low, and conversely, when transport to the north is high, so is sea level. Adjusted sea level data from the University of Hawaii Sea Level Center (http://www.soest.hawaii.edu/kilonsky/uhslc.html) were available for seven sites along the west coast of North America for the time period considered. Data were standardized for each station and converted to daily anomalies.

Temperature has often been assumed to be the most important environmental variable affecting biological processes. Average daily SST for each 1° box was obtained from the Comprehensive Ocean Atmosphere Data Set (Mendelssohn and Roy 1996). These data comprise real observations from ships and buoys. For this study, we

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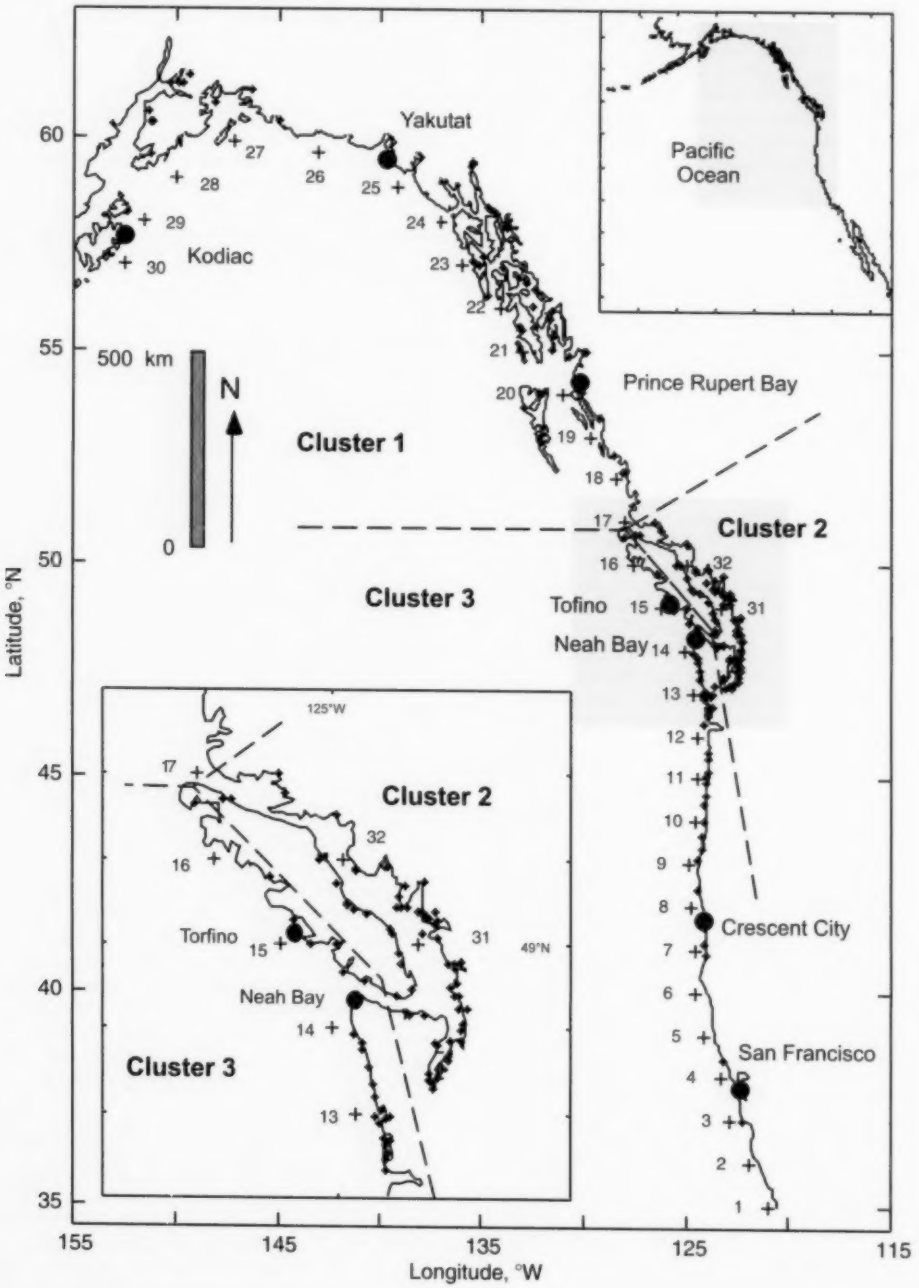
Fig. 1. Map of west coast of North America with the center of each 1° box (n = 32) indicated by a plus (+). The locations of the seven named sea level stations are indicated by the solid circles. The locations of the river mouths of the hatcheries releasing coded wire tagged coho salmon (*Oncorhynchus kisutch*) between 1973 and 1998 in each cluster are shown by stars (n = 225). The shaded Puget Sound – Strait of Georgia region is expanded in the lower inset map to show the boundary between cluster 2 and cluster 3. The upper inset map is of the west coast of North America with the study area shaded.



also used a derivative of subsurface temperature structure that we refer to as mixed-layer depth (MLD), which is a function of mixing energy and buoyancy input and refers to the zone of relatively homogeneous water formed by the history of mixing. Temperature has often been used to define the MLD, in part owing to the scarcity of salinity data and the ease of measurement reliability (Brainerd and Gregg 1995). In regions of relatively high freshwater input or seasonally variable salinity, this value may not represent the true MLD, but the seasonal thermocline is still a good measure of MLD (Brainerd and Gregg 1995). MLD was calculated from casts ar-

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chived in the World Ocean Database 98 Standard Level Temperature Profiles (Levitus et al. 1998). The individual temperature–depth observations in each 1° box were averaged to provide daily temperature-depth estimates. Only casts to depths greater than 100 m were included to remove shallow and nearshore casts where the MLD is often poorly resolved. MLD was defined as the depth (z) where the change in temperature (T) was most rapid, i.e., dT/dz was maximum. There is a correlation between MLD calculated from density data and the thermocline depth at Vancouver Island (G.W. Boehlert, unpublished data), supporting the use of this variable as a proxy for MLD. It is acknowledged that this measure of MLD may be less precise in the northern regions of this study, but it represents a useful proxy of subsurface structure related to MLD available for retrospective analyses of the kind performed here.

Matching biological and environmental data

The biological response variables considered within each cluster were survival, jack size from fish recaptured at the hatchery, and adult size of fish captured in the nearshore troll fishery. Restricting the environmental analyses to a single fishery allowed the actual size of fish to be used. Variation in these response variables attributable to environmental predictor variables was examined for three time periods. The first varied temporally and was specifically tailored to each individual hatchery release group. The time period began 10 days before and ended 30 days after the mean release day (some releases took place over 10 days). The second period considered was the 3 months when most jacks were returning to coastal waters close to the release region (July 1 – October 1 in the release year). The third time period was the 3 months when most adults were returning to coastal waters close to the release region (July 1 – October 1, year after release year). The peak time of adult coho salmon return varies from September to January, depending on the stock (Weitkamp et al. 1995), and so these time periods were chosen to include at least some marine residence time for all populations of returning jacks and adults.

For each time period, the environmental predictor variables were integrated in four different ways. The first measure was the mean value of the environmental variable. The second was the proportion of days in which an event greater than a threshold value occurred (i.e., upwelling > 0, standardized sea level > 0, v wind > 0 (northward event), SST > 12°C, (wind speed)^3 > 125 m^3·s^{-3}, and MLD > 30 m deep). The third and fourth measures were the cumulative sum of events greater (positive) and less (negative) than the same threshold values. For example, the positive sum of MLD was the sum of all daily MLD that were deeper than 30 m in the period of time considered. A large sum indicates a deep MLD over the time considered, whereas a small sum indicates a relatively shallow MLD. The use of positive and negative does not imply any predicted positive or negative effects on salmon but rather is used to approximately divide the range of environmental data in half.

Environmental conditions for each release period were calculated using the data from the 1° box closest to the release river mouth location. At this time, salmon are known to be in the release region. Environmental conditions at the time when jacks were returning were the daily average of the three closest 1° boxes to the release river. Environmental conditions at the time when adults were returning were created from the daily average from the five closest 1° coastal boxes to the release river mouth. The increasing spatial region over which environmental conditions were averaged reflects the relative uncertainty in the location of the returning jack and adult coho salmon.

The mean and proportion measures were calculated using the days for which environmental data existed in the time period considered. The cumulative positive and negative sums were calculated using the available data for the period of time being considered, with missing days being replaced by the mean for the period. If no environmental data existed for that release period, then the release was excluded during analysis using that variable.

Models

Preliminary exploration and analyses of these data via linear models often produced significant relationships but with very little variance in the response variable being explained by the predictor variable (most $R^2 < 10\%$). Scatterplots showed that many of the univariate relationships had nonlinear responses to the predictor variables. Multiple linear regression models were also attempted; again, although highly significant models were obtained, the variance explained by these models was generally less than 20%. Linear models relating size and survival to the environmental conditions will not be addressed further in this manuscript. Release weight was always significantly related to size and survival and was used in subsequent models.

Relationships between environmental and biological variables are often nonlinear (Cury and Roy 1989; Cury et al. 1995); however, present knowledge of the relationships does not always allow prediction of the form. For this reason, methods using the data to estimate the appropriate relationship are desirable. Iterative algorithms that extend linear multiple regression analysis to generalized additive models (GAM) have been used in several fisheries studies (Cury and Roy 1989; Cury et al. 1995). These methods, involving empirically estimated transformations of the data, provide a method for exploring the relationship between response and predictor variables when the form is unknown (Cury et al. 1995).

Analyses with nonlinear multiple regression models were used to explore the relationship between the response variables (size and survival) and the predictor variables (release weight and the nearshore environmental conditions) using the alternating conditional expectation (ACE) algorithm (Breiman and Freidman 1985; Cury and Roy 1989; Cury et al. 1995). ACE algorithms are iterative and allow transformations of both response and predictor variables. The partial residuals from the existing transformations of response and predictor variable relationships are calculated and transformations for the new variables are found.

Each of the three response variables (survival, jack size, and adult size) was modeled in each of the three possible time periods (release, jack return, adult return). This resulted in examination of eight general models (the influence of conditions on jack size in the adult year is nonsensical). To explore the relationships, each of the six environmental variables (calculated in four ways) was examined together with the release weight of fish for the eight models for each of the three regions found in the earlier cluster analyses. This resulted in $6 \times 4 \times 8 \times 3 = 576$ models of the form

$$\text{Response}_{\text{transformed}} = \text{release weight}_{\text{transformed}} + \text{environmental variable}_{\text{transformed}}$$

These models were examined for patterns in how and which environmental variables (including how they were measured) explained variance in the response variables in each of the three time periods and regions identified. "Best" models were selected by the simple criterion of maximum R^2 values. The relationships for environmental transformations were approximated with second-order polynomials, and these indicate the relationship between the particular environmental and response variables.

Results

A quality-controlled data set of 4382 releases of age-1 coho salmon made from 225 hatcheries for the years from 1973 to 1998 was obtained. Final size was obtained for 960 689 fish captured in the four fisheries. Most fish with size information were captured as adults after 1 year in the

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ocean (92.6%), with 4.2% captured as jacks. The remaining sizes were from fish returning in subsequent years and were not considered. A single release could have individual fish recaptured in all four fisheries; thus, there were 19 379 average return sizes calculated for the 4382 total releases.

Cluster analyses and spatial patterns in size and survival

The number of meaningful clusters found for each data set examined was either one or three (Table 1). Survival and adult size both produced three clusters, whereas the smaller data sets of jack size did not lead to any geographically meaningful clusters. The geographic identity and number of clusters identified for the two time periods (1973–1998 and 1980–1994) were the same. Geographic boundaries between clusters were obvious from the output and were the same for survival and adult size. Three geographically distinct clusters were created from these similar results. All hatcheries, including those with fewer than 9 years of data, were allocated to one of the three cluster regions according to the geographic location of the river entering the ocean (Fig. 1). The break between the northern (1) and other clusters (2 and 3) was at the northern end of Vancouver Island (51.5°N). The Puget Sound – Strait of Georgia cluster (2) included all hatcheries in the Strait of Georgia and Puget Sound between the northern tip of Vancouver Island and Neah Bay, Washington (WA), at 48.5°N. Cluster 3 was hatcheries from the northern tip of Vancouver Island to California. An average of 71% of hatcheries originally in the northern cluster (cluster 1), 84% originally in Puget Sound – Strait of Georgia (cluster 2), and 96% originally in the south (cluster 3) remained in the same cluster after geographic realignment. The final clusters consisted of 51 hatcheries in cluster 1 (1140 releases), 93 in cluster 2 (1559 releases), and 81 in cluster 3 (1683 releases) (Fig. 1).

The distinctness of the clusters differed between years for both jack and adult size and survival. Standardized jack size was almost never different between regions, as expected from the lack of geographic pattern in the jack size cluster analysis. Adult size and survival were distinct between clusters in over half of the years, but not always the same year (Fig. 2). This is consistent with the general lack of correlation among survival, jack size, and adult size; the only significant correlation (positive) occurred between survival and jack size in cluster 2 (Table 2). Significant correlations between clusters were limited to the coastal clusters 1 and 3. Furthermore, as might be expected, survival in cluster 3 was significantly correlated with survival from the Oregon Production Area (OPI, see Nickelson 1986) during the time period when both were available (1974–1996, $r = 0.67$, $p < 0.0005$).

The average standardized survival, jack size, and adult size varied between years (Fig. 2). There was a significant linear decline in survival in releases made in Puget Sound – Strait of Georgia (cluster 2) and an almost significant ($p = 0.0515$) decline in the south (cluster 3), whereas in the north (cluster 1), there was no significant trend in survival (Table 3). Jack size declined significantly through time in cluster 1, declined nonsignificantly in cluster 2, and showed no trend in cluster 3. Adult size also declined significantly in cluster 2 but not in the other two regions. In the cases with a significant decline, the linear regression (year) explained 19–46% of the variance in the response variable (Table 3).

Comparison of the relationship between survival, jack size, and adult size in each cluster shows they were impacted differently in the same years (Fig. 2). For example, in 1983, jack and adult size, but not survival, were below average in the south. Adult size and survival in the south was also low in 1992. There was little coherence in the other two regions in survival and adult or jack size (Table 2).

Important environmental variables: all models

All 576 models were initially evaluated to examine (*i*) the time period most strongly influencing survival and growth on average, (*ii*) the best method of calculating the environmental variable (mean, positive or negative sum, or proportion), and (*iii*) the most important environmental variable in the analyses. The metric used for this evaluation was the mean of the R^2 values for the appropriate subset of the 576 models. For example, to determine the most important time period in cluster 1, the average of the 24 models (each using one of six environmental variables, calculated four ways) was calculated for each of the three time periods, and the time period with the highest average R^2 was defined as most important.

This analysis suggested that survival in all three regions was influenced most by environmental conditions at some time after release, not by conditions at the time of release (Table 4). Models with survival as the response variable explained most variance when environmental variables from the time when jacks were returning (July–October, release year) were used in clusters 2 and 3, whereas in the northern cluster, environmental conditions when adults were returning (July–October, following year) explained more variance in survival. Comparing between clusters, survival was influenced most by environmental conditions in the south, then in the north, and least in the Puget Sound region. Jack size was most influenced by environmental conditions at the time of jack return in the south (cluster 3) and by conditions during release in cluster 2, whereas in the north, the same amount of variance was explained in both periods. Models for cluster 1 explained more variance in jack size than in the other clusters. Adult size was related most to environmental conditions at times after release, in the adult return period in cluster 2 and in the jack period in clusters 1 and 3. As for survival, models in cluster 3 explained the most variance in adult size (Table 4).

In a similar way, the most variance in the response variables was explained by models using environmental variables calculated as the sum of positive or negative events, rather than by using the mean, or proportion of days above a threshold value (Table 5). This suggests that it is the sum of conditions above or below a threshold experienced over a period of time that influence salmon size and survival, rather than mean conditions.

The most important environmental variable as indicated by the highest average amount of variance explained using all of the nonlinear models was MLD (Table 6). In eight of the nine cases, models using MLD explained on average more variance than the other environmental variables. For survival and jack and adult size, models incorporating variation in MLD explained most variance in clusters 1 and 3 and

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Table 1. Maximum number of geographically meaningful clusters formed from analyses of the coho salmon (*Oncorhynchus kisutch*) releases.

Data set	No. of hatcheries (no. of hatchery years)	No. of clusters identified
Survival clusters		
% survival, all hatcheries	225 (1716)	NA
% survival, 1980–1994	54 (653)	3
% survival, 1973–1998	76 (1120)	3
Adult size clusters		
Adult, all fisheries	186 (1577)	NA
Adult, all fisheries, 1980–1994	47 (560)	3
Adult, all fisheries, 1973–1998	73 (1037)	3
Jack size clusters		
Jack, all fisheries	118 (842)	NA
Jack, all fisheries, 1980–1994	23 (259)	1
Jack, all fisheries, 1973–1998	37 (473)	1

Note: The number of clusters is reported as 1 if no geographically meaningful clusters were found. The number of hatcheries and total years of release or final size data available before selection of hatcheries with more than 9 years data for either time period is shown. Hatcheries with just a single year of data could not be standardized, and so the number of standardized hatcheries was less than the total number. NA, not applicable.

least in cluster 2. Sea level was most important in influencing survival in cluster 2 and was also the second most important variable in the other regions. Least variance was explained in cluster 2 for all environmental variables.

Important environmental variables: best models

Although the analyses of the average model values indicate general patterns, they do not reveal the relationship between the response variables and the environmental variables. To do this, the best nonlinear additive models (highest R^2) that used more than 50 observations were chosen for the eight general models in each of the three clusters (n = 24 best models). The most common method of calculating the environmental variable was the sum of positive (n = 14) or negative (n = 7) daily events in the period of time considered. The mean value was used in two models, whereas the proportion of days above the positive value was used as the method of calculation in only one of the 24 best models. Thus, in the final consideration of the best models, only the best models that used the sum of positive or negative conditions were used, i.e., the three best models that used the mean or proportion were replaced with the next best model that used the positive or negative daily sum. After this adjustment, positive daily sum models accounted for 17 of 24 models.

These 24 best nonlinear models in the three regions had a mean R^2 = 0.60 and were based on an average of 201 releases and 18 years of releases. The best models differed with regard to the most important time period for variability in size and survival compared with the analysis of the average values for all the models. In the north (cluster 1), the model incorporating environmental conditions at the time of return explained more variance in survival than the other time periods (Fig. 3*c*). Survival had most variability explained by models using environmental conditions at the time of release in the Puget Sound (Fig. 4*a*) and southern regions (Fig. 5*a*). Overall, the survival models with highest R^2 were found in cluster 3 followed by cluster 1. The most important time period for explaining variance in jack size was less clear. In the northern and southern regions, both time periods explained equal variance (Figs. 3*d* and 3*e*, Figs. 5*d* and 5*e*), whereas in the central cluster (Puget Sound – Strait of Georgia), the model incorporating the conditions at the time of jack return explained more variance in jack size (Fig. 4*e*). As for survival models, models in clusters 1 and 3 best explained variance in jack size. Variation in adult size was explained best by the models incorporating environmental conditions at the time of release in all three regions (Figs. 3*f*, 4*f*, 5*f*), with cluster 3 better than cluster 1 better than cluster 2.

The most important environmental variable in each best model was similar for all clusters. MLD was the most important variable in four of eight best models in all three clusters, whereas sea level was chosen in one model in cluster 1, four models in cluster 2, and three models in cluster 3. SST was chosen twice in cluster 1 and once in cluster 3, and (wind speed)^3 was chosen once in cluster 1. None of the other variables was ever used in the best models.

The transformations for each best model in the most important time period show the nature of the relationship between the environmental variable and each response variable. These relationships were approximated with a second-order polynomial as an indication of the shape, and these explained an average of 41% of the transformation variance. In cluster 1, survival decreased as the sum of daily MLD less than 30 m increased (Fig. 3*c*). Jack size decreased with increasing sum of daily negative (wind speed)^3 (daily (wind speed)^3 < 125 $m^3 \cdot s^{-3}$) at the time of release (Fig. 3*d*). At the time of jack return, jack size at first declined with increasing positive sea level and then increased (Fig. 3*e*). Adult size increased with increasing sum of daily values of SST > 12°C at the time of release (Fig. 3*f*).

In cluster 2, although a different time period was more important, a decrease in survival was also associated with an increase in the sum of the daily MLD when depth was below 30 m at the time when smolts first entered the ocean (Fig. 4*a*). Jack size was greatest when the sum of positive daily MLD during the time of return was intermediate (Fig. 4*e*). Adult size in cluster 2, however, increased as the sum of the MLD when depth was below 30 m at the time when smolts first entered the ocean increased (Fig. 4*f*).

In the south (cluster 3), survival also decreased with an increase in the sum of daily MLD below 30 m at the time of release (Fig. 5*a*). As mentioned earlier, variance in jack size was explained equally by conditions at the time of release and the time of return. A slight increase in the sum of daily MLD > 30 m at the time of return was associated with larger jack size (Fig. 5*e*), whereas an increase in the sum of daily SST > 12°C at the time of release was associated with decreased jack size (Fig. 5*d*). An increase in the sum of daily MLD > 30 m during the time of release was associated with an increase in adult size in the south.

Inspection of the remaining model relationships at the less important time periods for each response variable shows a range of other relationships. For example, an increase in

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Fig. 2. Average standardized cluster values by year for coho salmon (*Oncorhynchus kisutch*). (*a*) Survival cluster averages by release year. Squares represent the northern cluster, diamonds the Puget Sound – Strait of Georgia cluster, and triangles the southern cluster. (*b*) Jack size cluster averages by return year. Symbols as in *a*. (*c*) Adult size cluster averages by return year. Symbols as in *a*. The solid portions of the bars at the base of each panel indicate when the annual cluster values were not significantly different, whereas the open bars indicate when the clusters were distinct (via analysis of variance).

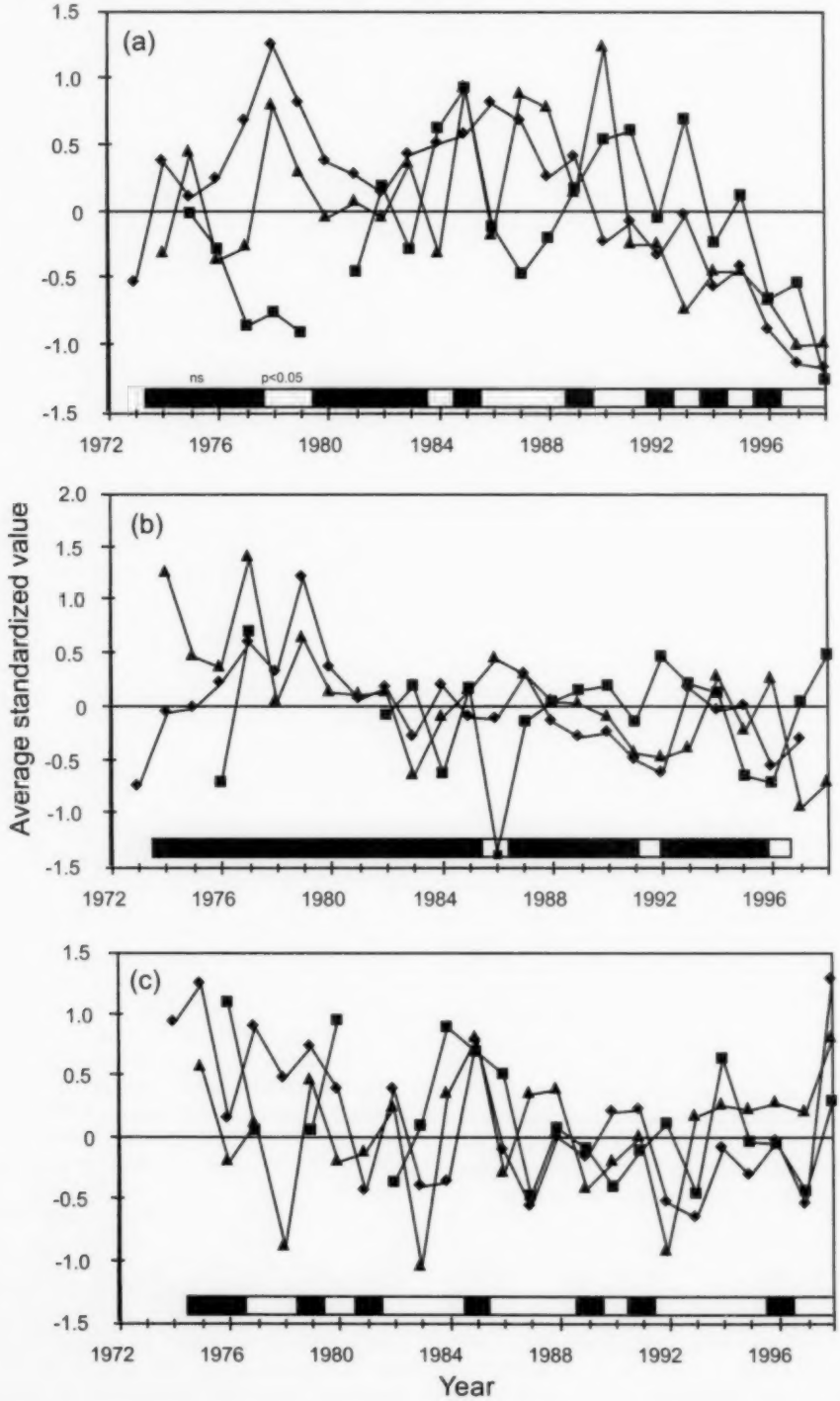

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Table 2. Correlation coefficients (Pearson's *r*) between annual values of survival, jack size, and adult size within and between clusters for coho salmon (*Oncorhynchus kisutch*).

		Region								
		Cluster 1			Cluster 2			Cluster 3		
Region	Factor	Survival	Jacks	Adults	Survival	Jacks	Adults	Survival	Jacks	Adults
Cluster 1	Survival	×								
	Jacks	–0.13	×							
	Adults	0.04	–0.33	×						
Cluster 2	Survival	0.10	–0.17	0.24	×					
	Jacks	–0.37	0.03	0.16	0.61***	×				
	Adults	–0.27	0.29	0.27	0.11	0.36	×			
Cluster 3	Survival	0.22	0.13	–0.09	0.60***	0.15	0.13	×		
	Jacks	–0.18	–0.14	0.24	0.52**	0.51*	0.46*	0.20	×	
	Adults	0.03	0.00	0.01	–0.29	0.28	0.41*	–0.13	0.19	×

Note: Significant correlation coefficients: *, 0.05; **, 0.01; ***, 0.001.

Table 3. Results from linear regressions on annual average standardized survival and jack and adult size through time in each cluster for coho salmon (*Oncorhynchus kisutch*).

Relationship	df	Slope	*F* statistic	*p*	R^2
Survival					
Cluster 1	22	0.0061	0.1211	0.7313	0.0057
Cluster 2	25	–0.501	15.601	**0.0006**	0.394
Cluster 3	24	–0.0322	4.2184	0.0515	0.155
Jack size					
Cluster 1	18	0.007	0.1291	0.7237	0.0075
Cluster 2	25	–0.0208	3.5720	0.0715	0.133
Cluster 3	24	–0.501	19.472	**0.0002**	0.4585
Adult size					
Cluster 1	20	–0.0294	3.7927	0.0664	0.1664
Cluster 2	25	–0.0347	5.5725	**0.0271**	0.1950
Cluster 3	23	0.0121	0.671	0.4215	0.0296

Note: Significant *p* values are shown in bold font.

Table 4. Most important time period for calculating the environmental variables using all of the non-linear models for coho salmon (*Oncorhynchus kisutch*).

Response variable	Time period	Cluster 1 (North)	Cluster 2 (Puget)	Cluster 3 (South)
Survival	Release	0.331 (471)	0.217 (698)	0.330 (254)
	Jack	0.357 (517)	**0.306** (741)	**0.443** (272)
	Adult	**0.395** (507)	0.304 (732)	0.425 (272)
Jack size	Release	**0.691** (75)	**0.329** (135)	0.488 (143)
	Jack	**0.691** (78)	0.323 (142)	**0.524** (153)
	Adult period	NA	NA	NA
Adult size	Release	0.408 (436)	0.185 (661)	0.410 (230)
	Jack	**0.416** (480)	0.216 (704)	**0.471** (247)
	Adult	0.383 (468)	**0.226** (702)	0.442 (249)

Note: The most important period in each cluster is indicated by the highest mean R^2 for the three cells (bold type). The mean R^2 (and number of observations per model) in each cell was calculated from the 24 models for each time period and response variable combination in each cluster. Each model in the group used a different environmental variable calculated in one of four possible ways. NA, not applicable.

negative sea level sums (i.e., lower sea level) was associated with increased adult size in the south (Figs. 5*g* and 5*h*).

Release weight and size and survival

The transformation relationships (graphs for these transformations are available on request) for release weight indicate that in the north (cluster 1) survival increased with an increase in release weight, whereas in the southern and Puget Sound clusters survival first declined as release weight approached about 30 g and then increased. There is a difference in the weight of fish released, with smaller fish being released in the north. Jack size increases with increasing release weight up to about 40 g in all three regions. In clusters 2 and 3, where larger smolts were released, jack size then declines as release weight increases above about 50 g. Adult size increases with release weight in all three regions,

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Table 5. Most important method of calculating the environmental variables using all of the nonlinear models for coho salmon (*Oncorhynchus kisutch*).

Response variable	Method	Cluster 1 (North)	Cluster 2 (Puget)	Cluster 3 (South)
Survival	Mean	0.357 (512)	0.276 (745)	0.398 (275)
	Negative	0.361 (491)	**0.292** (710)	**0.418** (261)
	Positive	**0.410** (479)	0.288 (693)	0.403 (254
	Proportion	0.316 (512)	0.248 (745)	0.378 (275)
Jack size	Mean	0.711 (75)	0.291 (143)	0.526 (153)
	Negative	0.706 (72)	0.345 (137)	0.499 (145)
	Positive	**0.716** (79)	**0.368** (132)	**0.540** (141)
	Proportion	0.630 (81)	0.299 (143)	0.458 (153)
Adult size	Mean	0.386 (474)	0.208 (711)	0.454 (250)
	Negative	0.419 (455)	0.220 (676	0.453 (238)
	Positive	**0.426** (443)	**0.225** (659)	**0.457** (230)
	Proportion	0.381 (474)	0.183 (711)	0.400 (250

Note: The most important method for each response variable in each cluster is indicated by the highest mean R^2 for the set of four cells (bold type). The mean R^2 (and number of observations per model) in each cell was calculated from the 18 (12 for jacks) models for the environmental and response variable combination in each cluster. Each model in the group used a different environmental variable calculated in three (two for jacks) different time periods.

Table 6. Most important environmental variable using all the nonlinear models for coho salmon (*Oncorhynchus kisutch*).

Response variable	Environmental variable	Cluster 1 (North)	Cluster 2 (Puget)	Cluster 3 (South)
Survival	MLD	**0.559** (121)	0.324 (524)	**0.482** (185)
	Sea level	0.377 (548)	**0.353** (649)	0.457 (262)
	v wind	0.271 (653)	0.259 (840)	0.386 (299)
	(Wind speed)^3	0.268 (653)	0.242 (840)	0.373 (299)
	Upwelling	0.329 (571)	0.239 (777)	0.359 (285)
	SST	0.361 (446)	0.239 (710)	0.338 (267)
Jack size	MLD	**0.741** (18)	**0.446** (86)	**0.590** (94)
	Sea level	0.712 (84)	0.409 (122)	0.509 (145)
	v wind	0.655 (91)	0.29 (167)	0.446 (169)
	(Wind speed)^3	0.716 (91)	0.258 (167)	0.446 (169)
	SST	0.641 (67)	0.295 (138)	0.556 (151)
	Upwelling	0.699 (87)	0.257 (153)	0.488 (161)
Adult size	MLD	**0.644** (114)	**0.257** (520)	**0.522** (176)
	Sea level	0.375 (501)	0.222 (620)	0.491 (234)
	v wind	0.324 (607)	0.210 (770)	0.416 (268)
	(Wind speed)^3	0.329 (607)	0.175 (770)	0.347 (268)
	SST	0.403 (411)	0.205 (705)	0.416 (248)
	Upwelling	0.340 (530)	0.185 (749)	0.452 (260)

Note: The most important variable in each cluster is indicated by the highest mean R^2 for the six cells (bold type). The mean R^2 (and number of observations per model) in each cell was calculated from the 12 (8 for jacks) models for the environmental method and response variable combination in each cluster. Each model in the group used a different environmental method calculated in three (two for jacks) different time periods. Abbreviations are MLD (mixed-layer depth) and SST (sea surface temperature).

although at very large release weight in the south, adult size does decline. In general, there is an increase in survival and size with increasing release weight in all regions.

Discussion

This exploratory analysis of the common patterns in size and survival and the environmental variables that most influence these response variables yielded some important insights into the mechanisms that produce the observed variance. The exploratory nature and methods used to understand these relationships preclude the use of statistical tests to separate between particular effects, instead the relative explanatory power of each model was used as the guide to select the most important patterns.

Spatial and temporal trends in size and survival

The geographically meaningful clusters formed by the cluster analysis based on survival and adult size identified the same three regions. The break between the northern and southern cluster at the tip of Vancouver Island identified in this study matches the transition between the upwelling and downwelling regions of the west coast, also coinciding with an important boundary between fishery production domains (Ware and McFarlane 1989).

Patterns of jack size did not reveal distinct regions, perhaps because there was insufficient data to resolve the pattern or there is a threshold size for jacks that results in a smaller range of jack sizes. In the latter case, this smaller dynamic range of jack size would make detecting consistent spatial patterns in the cluster analysis more difficult. Adult

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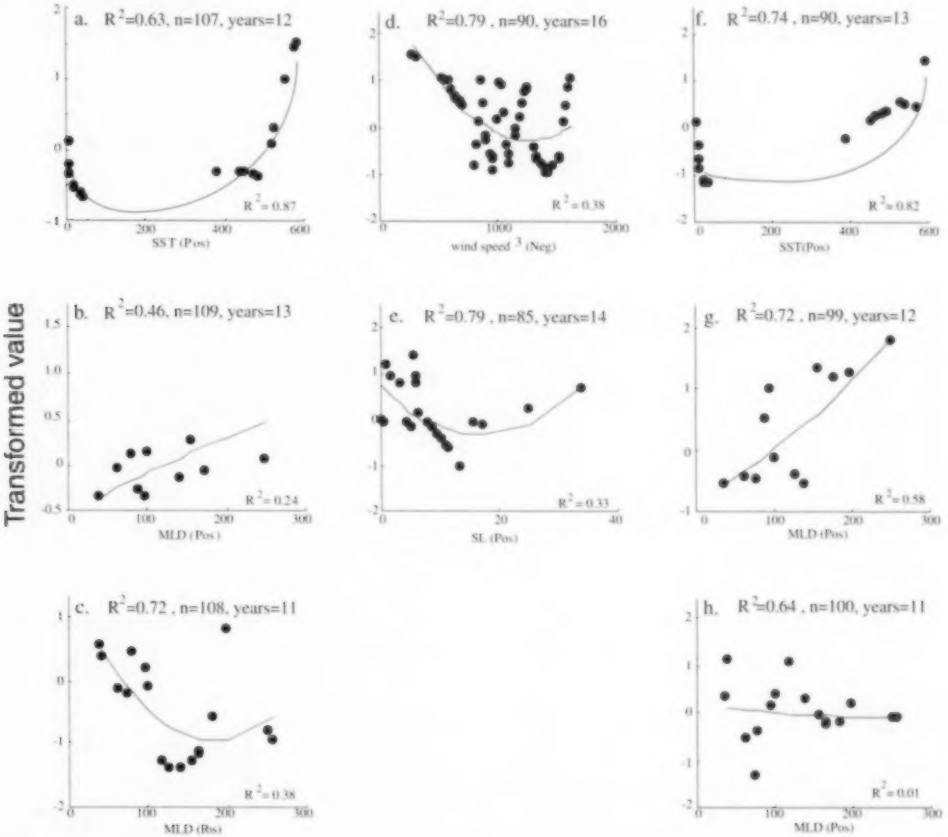
Fig. 3. Cluster 1 (north) environmental variable transformations from the best nonlinear model (highest R^2). The R^2 for the model, number of observations, and number of years that the observations covered are shown at the top of each panel. The environmental variable and calculation method for each best model is indicated on the *x* axes. The shape of each transformation relationship indicates the relationship of the environmental variable to each response variable, and these have been approximated with second-order polynomials. The R^2 for these fitted polynomial relationships is also shown for each panel. The response variable and time period for the environmental variables for each panel are (*a*) survival, release period; (*b*) survival, jack return period;. (*c*) survival, adult return period; (*d*) jack size, release period; (*e*) jack size, jack return period; (*f*) adult size, release period; (*g*) adult size, jack return period; (*h*) adult size, adult return period. The relationship between jack size at return and environmental conditions when adults return was not examined, as it had no biological basis.



size produced the same clusters as did survival, suggesting commonalities in the regions where the fish are residing during the ocean period of their life cycle. Thus, both adult size and survival are influenced by conditions in the same region, although it is not possible to tell from cluster analysis if common physical factors produced the patterns. Furthermore, the annual patterns of survival, jack size, and adult size in each region showed that different responses occurred in the same year.

The results of the cluster analyses support the a priori division between coastal Washington and Oregon and Puget Sound salmon used in previous studies of survival (e.g., Coronado and Hilborn 1998; Beamish et al. 2000). On the outer coast, the division between clusters 1 and 3 is also consistent with the division in coherence of upwelling favorable winds in summer and with the changes in British Columbia salmonid survival noted by Welch et al. (2000). It is also near the bifurcation of the Subarctic current into the California and Alaska currents. Interannual differences in either the latitudinal position of this bifurcation or the relative proportion of water entering these two currents might affect salmon ocean survival through effects on prey production or on salmon distribution and migration (Chelton 1984).

The decline in survival of CWT hatchery-released coho in the south (cluster 3) over the last 20 years was similar to that reported elsewhere (e.g., Coronado and Hilborn 1998; Beamish et al. 1999) and has occurred despite large increases in the release of hatchery fish (e.g., Mahnken et al. 1998). Despite possible freshwater and hatchery influences, unfavorable ocean conditions are thought to be largely responsible (Coronado and Hilborn 1998; Mahnken et al. 1998).

Role of environmental variation in size and survival

Different patterns for size and survival in common regions suggest that the same set of environmental variables may be acting in different ways on the different life stages of coho

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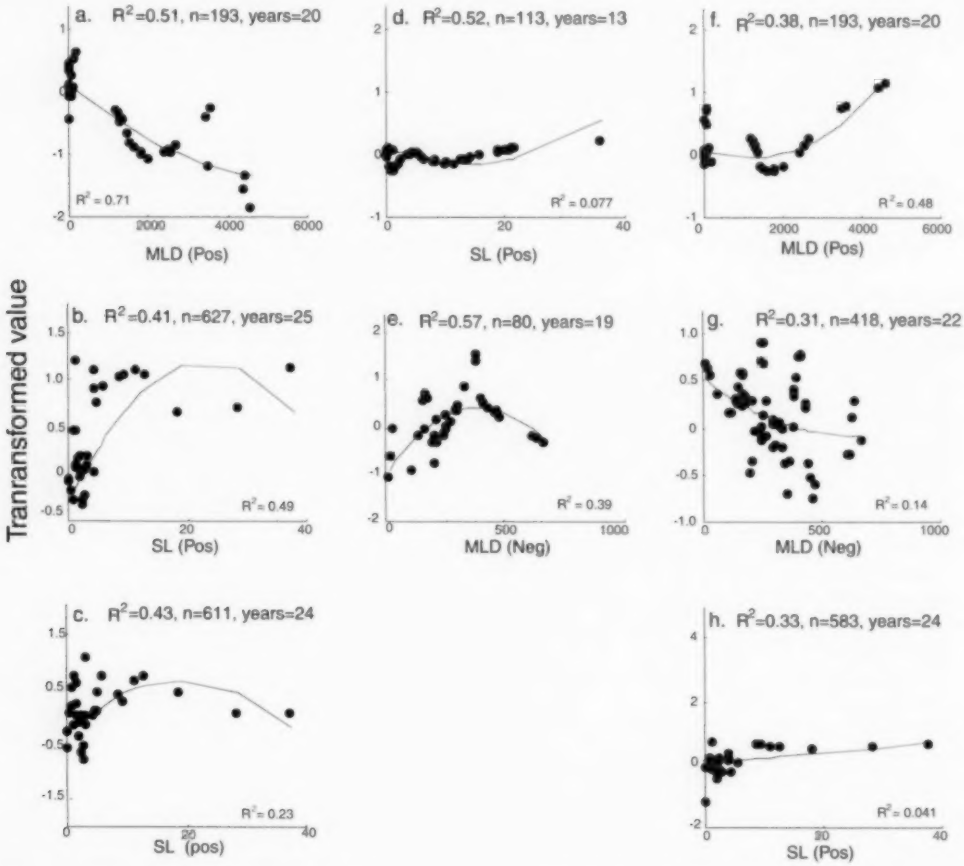
Fig. 4. Cluster 2 (Puget Sound – Strait of Georgia) environmental variable transformations from the best nonlinear model (highest R^2). The R^2 for the model, number of observations, and number of years that the observations covered are shown at the top of each panel. The environmental variable and calculation method for each best model is indicated on the x axes. The shape of each transformation relationship indicates the relationship of the environmental variable to each response variable, and these have been approximated with second-order polynomials. The R^2 for these fitted polynomial relationships is also shown for each panel. The response variable and time period for the environmental variables for each panel are (*a*) survival, release period; (*b*) survival, jack return period; (*c*) survival, adult return period; (*d*) jack size, release period; (*e*) jack size, jack return period; (*f*) adult size, release period; (*g*) adult size, jack return period; (*h*) adult size, adult return period. The relationship between jack size at return and environmental conditions when adults return was not examined, as it had no biological basis.



salmon. Nonlinear models were used in an exploratory manner to identify the most important single environmental variable associated with variance in salmon survival and size. The increase in variance explained by nonlinear additive models over linear multiple regression using the ACE algorithm depends on the degree of nonlinearity in the relationship. Inspection and analysis of the transformation plots during analyses showed that most of the relationships were better described by log or polynomial functions than by linear relationships.

The amount of variance explained by models using environmental conditions during different time periods of a salmon's ocean life showed that the influence of environmental conditions on size and survival was not always greatest when the fish were first released. Consideration of all the models suggested that survival was, on average, explained best by models that incorporated environmental variability at times after release. Similarly, considering the average of all models, jack and adult size were influenced most by conditions after release.

Overall, calculating the environmental variables as the total amount of the condition above or below a threshold in the time period led to models explaining more variance than models using mean or proportional measures of the variables. Conceptually, this is similar to the degree-day idea in developmental biology; a similar approach has been used to explain effects of environmental variability on appendicularian abundance (Taggart and Frank 1987) and coho survival (Cole 2000). Most studies just use mean conditions to describe the environment; these results suggest that other approaches like cumulative conditions should be considered. Analyses based on the average of all models may be problematic as this approach requires that all environmental variables or all time periods be averaged together. Different environmental variables may act most strongly at different

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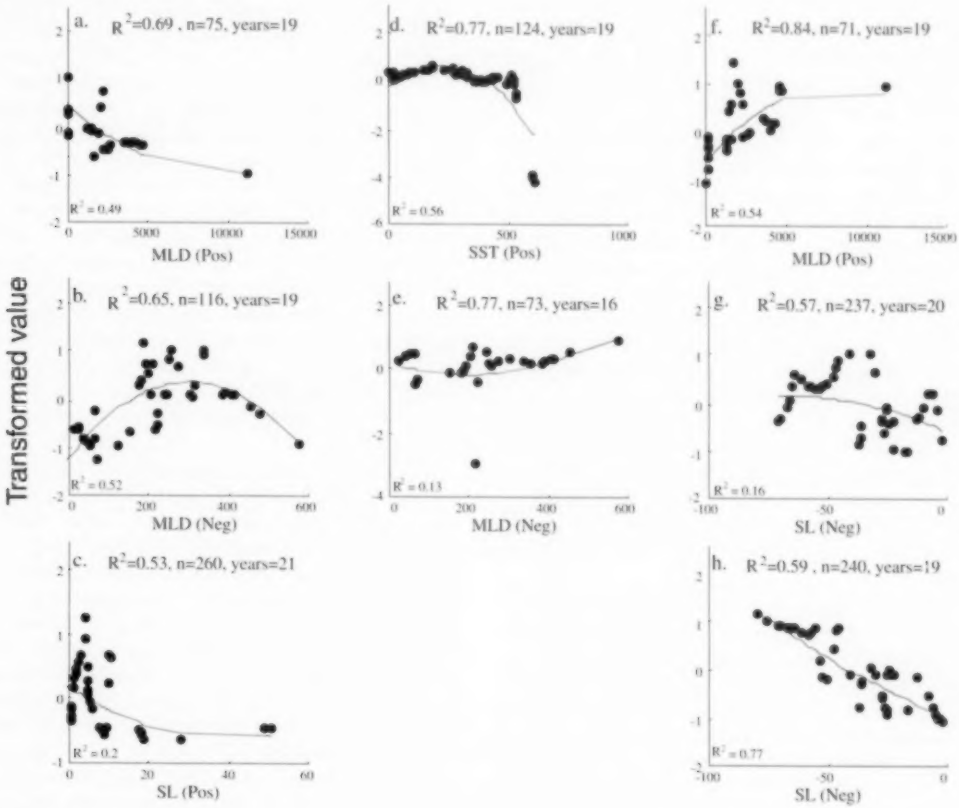
Fig. 5. Cluster 3 (south) environmental variable transformations from the best nonlinear model (highest R^2). The R^2 for the model, number of observations, and number of years that the observations covered are shown at the top of each panel. The environmental variable and calculation method for each best model is indicated on the x axes. The shape of each transformation relationship indicates the relationship of the environmental variable to each response variable, and these have been approximated with second-order polynomials. The R^2 for these fitted polynomial relationships is also shown for each panel. The response variable and time period for the environmental variables for each panel are (*a*) survival, release period; (*b*) survival, jack return period; (*c*) survival, adult return period; (*d*) jack size, release period; (*e*) jack size, jack return period; (*f*) adult size, release period; (*g*) adult size, jack return period; (*h*) adult size, adult return period. The relationship between jack size at return and environmental conditions when adults return was not examined, as it had no biological basis.



times of a salmon's ocean life. To understand which environmental variable acts most strongly at each time, the models were considered separately for each time period.

The best models (highest R^2) incorporated the sum of positive or negative events, indicating that the total amount of the conditions experienced was most important, not the mean conditions during the period of time considered. Analysis of the best models showed that survival was most influenced by variance in conditions at the time of release in cluster 2 (Puget Sound – Strait of Georgia) and cluster 3 (south) and at the time of return in cluster 1 (north). This contrasted with the pattern uncovered by considering the average of all models, which suggested that later time periods were more important in all regions. The most important time period for environmental influence of jack size from consideration of the best models was also different. Environmental conditions in the two time periods that might influence jack size, during release and during jack return, explained similar amounts of variance. Again, in contrast to the pattern using all models, the best models revealed that most variance in adult size was explained by models that incorporated environmental data during the time of release in all three regions. The greatest success in explaining variance via environmental variables was in the south and north; Puget Sound – Strait of Georgia models did most poorly. This suggests that either environmental variation is less important in this area or more important environmental variables were missed (discussed further below). Otherwise, these central populations have a reasonably close relationship with biological features in the south.

The most important environmental variable, as indicated by the highest average amount of variance explained by the best models, was MLD, used 12 out of 24 possible times. The mixed layer is the result of the cumulative effects of turbulence in the mixing layer (Brainerd and Gregg 1995) and factors affecting stratification such as freshwater inputs and seasonal warming. The upper mixed layer is separated from deeper waters by a change in density that impedes dif-

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fusive mixing of nutrients across the boundary. Interannual changes in MLD have been cited as the mechanism through which variation in the atmosphere produces variation in the biological properties of the ecosystem (Venrick et al. 1987; Polovina et al. 1995). A shallow mixed layer (as indicated by a small sum of daily MLD > 30 m) was associated with increased survival in all three regions. A shallow mixed layer is typically associated with increased plankton production (Polovina et al. 1995), which is likely to promote survival (as observed here), whereas a deeper mixed layer may be associated with reduced production of the zooplankton, which may in turn reduce salmonid survival (Parsons and Kessler 1987). A deeper mixed layer may also increase the relative dispersion of prey (Lasker 1981).

In contrast to survival, a deeper MLD was associated with larger adult size in the most important time period in clusters 2 and 3 (and in cluster 1, but not in the most important time period), and larger jack size in cluster 3. This indicates that conditions promoting increased survival (e.g., shallow MLD) may not lead to increased size. Differing trends of survival and size tempt one to consider density-dependent mechanisms. Limited evidence does suggest that density-dependent mechanisms operate on coho (Emlen et al. 1990; Ogura et al. 1990, but see Nickelson 1986) and chinook (Beamish et al. 1995) salmon during the marine phase. The finding that MLD was important in all three regions yet that the three regions had temporally differing patterns of size and survival suggests that MLD may vary temporally between these regions. In fact, average MLD is uncorrelated between the three regions (L. deWitt, Pacific Fisheries Environmental Laboratory, 1352 Lighthouse Ave., Pacific Grove, CA 93950, personal communication).

Sea level was the second most important environmental variable, as shown by the analysis of all of the models and of just the best models, when it was used eight times. In general, inspection of the transformation relationships from the best models showed that lower sea level was associated with both increased fish size and survival in the south but was less important in the north. Lower sea level is associated with increased transport from the north and typically higher nutrient waters in the California current (McGowan et al. 1998). The sources waters from the Subarctic (North Pacific) current, however, may have varying nutrient content dependent on the proportion of water from subtropical origin, which depends on midlatitude wind stress (Parrish et al. 2000).

SST was the most important environmental variable in only three of the 24 best models, in which it was related to jack size in the southern cluster and to survival and adult size at the time of release in the northern cluster. Previous studies of environmental variation have implicated SST as an important influence on coho survival (e.g., Ryding and Skalski 1999; Cole 2000); however, the set of environmental variables considered here is greater. Although our results do not suggest that SST is unimportant, its effects appear less influential than MLD and sea level. SST is related to these variables, however, so it is possible that previous studies have found a correlative variable, rather than the underlying variable. Indeed MLD and sea level may in turn be correlated with a more primary and as yet unknown causative environmental variable.

Wind, measured as either the v component (the principal forcing for upwelling) or (wind speed)^3 (an index of mixing), was also less important for coho size and survival. Coho smolts may be too large when they enter the ocean to be affected by turbulence-induced disruption of prey aggregation as suggested for some marine fish larvae (Peterman and Bradford 1987). Upwelling was the least important variable in explaining variance in coho salmon size and survival. Upwelling was found to be an important predictor of coho survival before about 1981 (Nickelson 1986), but not afterwards (Pearcy 1992). Much of the data in this study is from releases after 1982 and so any effect of the previously reported upwelling relationship may be obscured.

Other environmental influences on salmon production not addressed in this study include freshwater inputs and plumes. Salmon abundance has been found to vary with river discharge in some regions (Pearcy 1992). River inputs may influence the distribution of smolts (e.g., advection), the physical environment (e.g., stratification), food availability, and predation risk (Pearcy 1992; Gargett 1997), all of which may affect size and survival. Freshwater input is likely to be important for the Strait of Georgia – Puget Sound area (Beamish et al. 1995), which did have the lowest variance explained by the set of environmental variables used in this study. The Columbia River exits in the area covered by cluster 3 and so runoff might also be important in this region (Pearcy 1992).

A biological response that we have not considered is the manner in which environmental factors influence migration. In a tagging study over a period of 7 years, Kallio-Nyberg et al. (1999) noted that environmental factors had a strong influence on migratory route in young Atlantic salmon and that prey abundance influenced migratory distances. Although our cluster results suggest that animals within clusters are influenced by coherent patterns of environmental variability, coho salmon may respond similarly and demonstrate interannual variability in spatial and temporal patterns of ocean utilization. Further research will be needed to address this question in coho salmon.

Scales of environmental variation

Biotic responses to environmental variation exist at several spatial and temporal scales, and analyses of potential relationships must take this into account. Changes at a large scale, the coupled ocean–atmosphere system, can lead to changes in those environmental variables used here, affecting primary production and food webs that support higher trophic production (Bakun 1999). Ultimately, environmental variation affects survival and growth at the individual level, and so consideration of small scales may best expose the causative environmental relationships.

In this study, we show that at the fine scale of individual salmon releases, environmental variables can account for variance in size and survival, two components of salmon production. Three larger spatial regions along the coast of North America where the size and survival of coho salmon has similar patterns were identified, suggesting that environmental variation acts similarly over these large regions.

The relationship observed between environmental and biological variables may change with increasing spatial and temporal scales and also over different time periods. For

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example, the regional relationship between upwelling and coho survival changed in the early 1980s (Nickelson 1986; Pearcy 1992). Koslow et al. (2001) showed that annual survival on a regional scale (measured as OPI) was related to a suite of variables and some of the relationships were opposite to those observed here. Their analysis extended over a longer period of time, and so changes in the relationships might be expected given the current understanding of regime shifts (Steele 1996; Hare et al. 1999; Beamish et al. 2000).

In fact, caution is required in examination of environmental relationships over a long period of time covering several regimes, because individual relationships that exist in one regime may be blurred or dominated by those existing in another period (Parrish et al. 2000). Analysis at the larger spatial and temporal scales, while providing for robust relationships, also risks obscuring the mechanisms responsible for variation, whereas at the smaller scales, too much variation can also obscure relationships. We accept that at different time periods than considered here, other variables may become more important or the same variables may act in different ways. Unfortunately, the exploratory nature of this study restricts the generalizations and inferences that may be made compared with a more statistical or hypothesis-driven study.

We have identified particular time periods and environmental variables that influence size and survival at a fine scale of individual salmon releases over a wide latitudinal range. Further understanding of the effect of variability in the coastal environment on survival and size at different life stages, however, requires improved knowledge of where, when, and how juvenile and adult salmon use particular habitats. This can come from experimental net captures, experimental fishing, traditional recovery-based tagging (including CWT), acoustic tagging, and trophic studies (Brodeur et al. 2000). In particular, our results and those of Koslow et al. (2001) suggest the importance of fieldwork to describe the biotic and abiotic conditions associated with mixed layers of varying depths in the regions identified here. This can be followed by experiments to examine how conditions in a shallow (deep) mixed-layer depth result in increased (decreased) survival and decreased (increased) size in coho salmon through exploration of physiological, feeding, competition, and predation relationships.

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Resource partitioning as a factor limiting gene flow in hybridizing populations of Dolly Varden char (*Salvelinus malma*) and bull trout (*Salvelinus confluentus*)

John Hagen and Eric B. Taylor

Abstract: Dolly Varden char (*Salvelinus malma*) and bull trout (*Salvelinus confluentus*) hybridize in areas of secondary contact in northwestern North America but maintain their genetic integrity in spite of gene flow. We examined juvenile stream ecology and adult reproductive ecology of these species in sympatry to test for specializations to alternative niches that may act as a basis for natural selection against hybrids. Juvenile Dolly Varden occupied deeper, faster water and foraged more during daytime in the drift, whereas bull trout used shallower, slower water and made more nighttime foraging attempts towards the substrate. The species showed extensive diet overlap (Schoener's index = 0.7–0.9), and we found evidence for density compensation between species among sites. Our results suggest no obvious basis for selection against hybrids at the juvenile stream-rearing life-history stage. Bull trout, however, are adfluvial, whereas Dolly Varden are permanent stream residents. Bull trout are also much larger at maturity (50–80 cm vs. 12–15 cm) and build redds in faster, deeper water using larger substrate sizes. Consequently, hybrid genotypes may be selected against in these alternative life-history niches or during reproduction owing to their intermediate size at maturity and size-dependent spawning habitat use and mate choice.

Résumé : La Dolly Varden (*Salvelinus malma*) et l'Omble à tête plate (*Salvelinus confluentus*) s'hybrident dans les régions de contact secondaire dans le nord-ouest de l'Amérique du Nord, mais ils maintiennent leur intégrité génétique malgré le flux de gènes. Nous avons étudié l'écologie des juvéniles dans les cours d'eau et de l'écologie de la reproduction des adultes de ces espèces dans des situations de sympatrie pour vérifier l'existence de spécialisations à des niches de rechange qui pourraient servir de base à une sélection naturelle contre les hybrides. Les juvéniles de la Dolly Varden vivent en eau plus profonde et plus rapide et font plus de recherche de nourriture pendant le jour, alors que l'Omble à tête plate occupe des eaux moins profondes et moins rapides et fait plus de tentatives de recherche de nourriture sur le substrat la nuit. Les deux espèces ont des régimes alimentaires qui se chevauchent considérablement (indice de Schoener = 0,7–0,9) et il y a des indices de l'existence d'une compensation de densité entre les espèces parmi les sites. Nos résultats n'identifient aucune base évidente pour postuler l'existence d'une sélection négative des hydrides au cours de la partie du cycle biologique correspondant au développement des juvéniles en eau courante. L'Omble à tête plate, cependant, fait des migrations vers les eaux stagnantes (c'est une espèce « adfluviale »), alors que la Dolly Varden réside en permanence dans les eaux courantes. Les ombles sont aussi beaucoup plus grands à maturité (50–80 cm contre 12–15 cm) et construisent leurs gravières en eau plus profonde et plus rapide, utilisant des substrats plus grossiers. Conséquemment, il peut y avoir une sélection négative des génotypes hybrides dans ces niches de rechange de développement juvénile ou alors durant la reproduction; les hybrides possèdent, en effet, une taille intermédiaire à maturité et leur utilisation des habitats de fraie et leur choix de partenaire sont des comportements reliés à la taille.

[Traduit par la Rédaction]

Introduction

Hybrid zones can be broadly defined as geographic areas where mating occurs between genetically distinct populations to produce individuals of mixed genetic ancestry (Arnold 1997; Jiggins and Mallet 2000). Although once considered rare in most animals, hybrid zones have long been recognized in various groups of fishes (Arnold 1997) and are viewed as excellent "natural laboratories" that provide opportunities to understand processes that maintain genetic

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distinction in the face of gene flow and perhaps the processes that lead to the evolution of reproductive isolation (Barton and Hewitt 1989; Jiggins and Mallet 2000).

Natural hybridization and introgression have been reported in a number of co-existing salmonid species in the Northern Hemisphere (e.g., reviewed by Verspoor and Hammer 1991). In most cases, the parental species appear to maintain their integrity in the face of hybridization and some gene flow (e.g., Verspoor and Hammer 1991; Baxter et al. 1997), but in some cases, hybrid swarms may develop (e.g., Forbes and Allendorf 1991). However, there have been no detailed studies of the potential genetic or ecological factors that might limit gene flow in salmonid hybrid zones. One hypothesis that could explain the maintenance of parental genomes in spite of gene flow is environment-dependent natural (or sexual) selection against hybrids in nature (Arnold 1997). Under this model, parental species are adapted to alternative niches and hybrids between species suffer reduced fitness if they are phenotypically intermediate to the parental species in traits important to exploitation of the parental species' niches (Arnold and Hodges 1995).

Two species of char, Dolly Varden (*Salvelinus malma*) and bull trout (*Salvelinus confluentus*), hybridize in several watersheds along a broad zone of secondary contact in northwestern North America (Taylor et al. 2001). In one area, Thutade Lake of the upper Finlay (Peace) River drainage, the two species interact in what appears to be a "bimodal" hybrid zone (sensu Jiggins and Mallet 2000) where most genotypes are either parental or backcrosses with relatively few F_1 hybrids (Redenbach 2000). Given that intrinsic (i.e., genetic) mechanisms of selection against hybrids appear to be absent in these species owing to high viability of laboratory crosses (Haas and McPhail 1991) and to the production of backcross genotypes in nature (Baxter et al. 1997; Redenbach 2000), hybrid zones between Dolly Varden and bull trout may represent a case where extrinsic (ecological) selection against hybrids may constrain gene flow between the species.

In this study, we examined the potential contribution of ecological factors to the maintenance of genetic distinction between the species. In most naturally co-existing salmonids, different species typically demonstrate strong resource partitioning as stream-resident juveniles (e.g., Ross 1986; Taylor 1991). If ecological selection is important to maintaining parental genomes in the face of gene flow, then this predicts that the parental species should exhibit distinct resource utilization along one or more ecological axes. We evaluated this prediction by testing for habitat, food, and time resource partitioning between co-existing juvenile Dolly Varden and bull trout in a pristine watershed in north-central British Columbia. Thus, two objectives of our study were to document, for the first time, the extent of resource partitioning between sympatric juvenile Dolly Varden and bull trout and to evaluate the extent of density compensation in areas of local sympatry and allopatry. Density compensation refers to the idea that co-existing species are so similar in resource use that reduced density or absence of one species is compensated for by an increase in the density of the other species while total fish density remains relatively constant. Consequently, the absence of density compensation would suggest that the species have evolved major differences in resource use such that the presence or absence of one species has little or no effect on the density of the other species. Finally, the reproductive phase of an individuals' life history also requires resource acquisition, e.g., in terms of habitat use. Consequently, our third objective was to test for habitat partitioning between Dolly Varden and bull trout during spawning by comparing size at maturity and habitat dimensions at identified spawning sites.

Materials and methods

Study area and design

The Thutade Lake watershed is situated near the Pacific–Arctic continental divide in north-central British Columbia, at approximately 57.0°N latitude and 126.7°W longitude (Fig. 1). Thutade Lake is the source of the Finlay River, a tributary of the Peace River and ultimately the Mackenzie River, which flows into the Arctic Ocean. The fish community is relatively simple, being dominated numerically by Dolly Varden and bull trout, although other native salmonids such as rainbow trout (*Oncorhynchus mykiss*), kokanee (*Oncorhynchus nerka*), and mountain whitefish (*Prosopium williamsoni*) also occur in small numbers in the tributary streams (Bustard 1999). At most sites, therefore, the potentially confounding effects of other competitors were not an issue. Because of the remote location of the Thutade watershed and the lack of fishing pressure or human-mediated habitat disturbance, the fish populations are also thought to be at levels that are close to the environment's natural carrying capacity, which was important for the assessment of the effects of interspecific competition. Importantly, gene flow between Dolly Varden and bull trout and hybrid fertility in the watershed have been documented. Hybridization occurs but is infrequent; 0.61% of all char examined were classified as F_1 hybrids, 4.8% as resulting from backcross matings, and 0.15% as post-F_1 hybrids (Redenbach 2000).

The life-history patterns of Dolly Varden and bull trout differ in the watershed and this influenced the design of our study. Dolly Varden reside in small streams for their entire life cycle. Bull trout spend up to 4 years in these same streams at the beginning of their lives but then migrate to Thutade Lake and become piscivorous. Consequently, we felt that it was important to consider both Thutade Lake and its tributary streams in our investigation of resource-use specializations. We sampled the lake environment to assess the apparent absence of Dolly Varden in this habitat and designed our sampling of the tributary streams around Schoener's (1974) three niche dimensions: habitat, food, and time, with the time dimension investigated by replicating habitat and food measures for day and night time periods. We assessed resource use along three habitat dimensions (water depth, mean current velocity, and hydraulic habitat type) and three food dimensions (foraging mode (benthic versus drift), mean prey item biomass, and taxonomic classification of prey).

Life history

To confirm the suspected migratory life-history differences between the species, we surveyed Thutade Lake between June 16 and June 21, 1998. We captured fish with small-mesh, monofilament tangle nets set both on the bottom and suspended from the surface at two different locations on the lake. From June 16 to June 18, we fished an open-water, deeper location adjacent to a large shoal, and from June 19 to June 21, we fished a shallower, more complex shoreline near the lake outlet. All fish captured were anaesthetized, identified, measured, and released. We sampled char stomach contents using the pulsed gastric lavage method (Foster 1977) and preserved them in a solution of 10% formalin for later measurements.

To assess species differences in reproductive ecology, body size data and tissue samples for molecular genetic analysis (Redenbach

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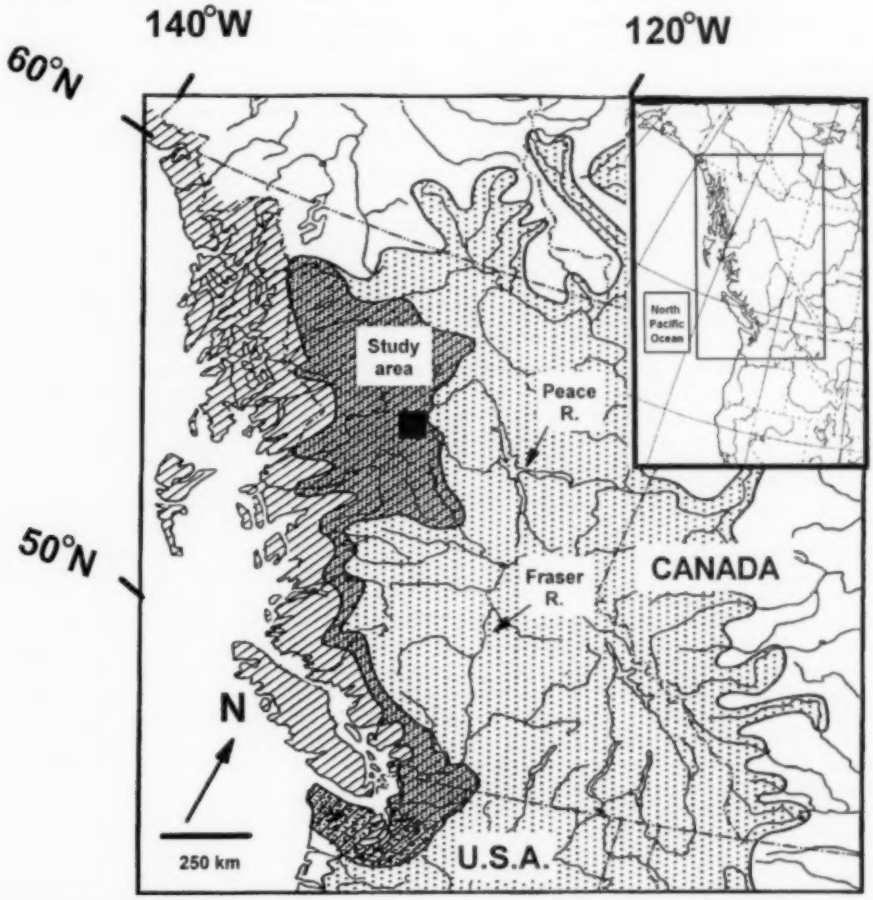
Fig. 1. Distributions of Dolly Varden, *Salvelinus malma* (hatched), and bull trout, *S. confluentus* (stippled), and areas of overlap (dark hatching and stippling) in western Canada. The study site is the Thutade Lake watershed (black square), located at approximately 57.0°N latitude and 126.7°W longitude at the source of the Finlay River (upper Peace River). The inset shows the general study area in relation to western North America.



2000) were collected during the bull trout spawning migration by angling at locations along the Attichika River and along its tributary Kemess Creek. The Attichika River accounts for most (about 60%) total adult bull trout abundance in the Thutade watershed (500–600 spawners annually, Bustard 1999). Adult Dolly Varden from throughout the watershed were also sampled, but because they were difficult to distinguish from immature char, we sacrificed a sample to determine maturity status of individuals by dissection. Spawning timing was investigated in the Kemess Creek watershed for both species in all years of a population-monitoring program undertaken from 1995 to 1998 (e.g., Bustard 1999). All known spawning areas in the watershed were surveyed on a weekly basis by foot over the spawning period for both species combined (early August until early October of each year). For each species, the numbers of spawners present in stream reaches were recorded, as was the cumulative total number of redds (spawning sites excavated into the stream substrate) on each survey date. A subsample of redds from the total number identified from three independent reaches for both species (Table 1) was compared in terms of hydraulic and substrate characteristics after spawning had been completed. Mean stream depth and current velocity were recorded as the average of two measures, each over undisturbed substrate on opposite sides of the midpoint of the redd. To minimize disturbance to incubating char embryos, particularly for bull trout where the substrate was imbedded, we limited our redd substrate size comparisons to estimates of surface substrate size. For each redd, we visually estimated a single substrate particle of "median-like" size, i.e., 50% of the remaining pieces were smaller than the selected pieces and 50% were larger. The maximum diameter of each selected piece was measured and constituted the D_{50} of substrate size for each redd. The D_{50} measure was not intended to represent the average substrate size within the total redd volume (which would require disturbing embryos) but rather an approximate quantification of differences in surface substrate size between species that appeared obvious by eye. Notwithstanding the approximate nature of substrate size measure, our data were consistent with substrate sizes of redds recorded for other populations of bull trout (e.g., Baxter and McPhail 1996) and with more detailed measures of interspecific differences in mean particle sizes for smaller numbers of redds (D. Bustard, Bustard and Associates, Smithers, B.C., personal communication). Spawning locations were recorded within 400-m marked sections of the surveyed reaches and also in smaller or seepage-fed tributaries located along these marked sections.

Resource use in tributary streams

Resource-use measurements in the tributary stream environment,

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for both species concurrently, were made during July and August 1998. The study reach was a 2.0-km section of North Kemess Creek, a third-order tributary of the Attichika River (which in turn flows into Thutade Lake) and an area of known, strict sympatry. We used snorkel surveys to locate and observe individual fish of each species. If the snorkeler deemed the fish undisturbed, he observed it for 5 min and recorded the number of surface, drift, and benthic foraging attempts as well as the species identification. The fish was then captured using two large aquarium nets and measured, its adipose fin was clipped for genetic analysis, and the fish was then preserved in a solution of 10% formalin for laboratory gut content analysis. At the focal point (nose-point location) for each fish, we measured stream depth and mean current velocity and also noted hydraulic habitat type (riffle or pool, main channel or side channel). In habitats too shallow for snorkel observations, we used a battery-powered electrofisher and short pulses of electricity to capture individual fish. Depth, velocity, and hydraulic habitat type were recorded and the fish was sampled as above. The location of focal points through electrofishing is obviously less precise than through diver surveys, but the resulting relationships, even though less precise, would provide more accurate overall conclusions by including all available habitats.

We replicated underwater observations at nighttime using a diver's light shining through a sanded translucent red filter that minimized disturbance to fish (Heggenes et al. 1993) and sampled fish by electrofishing at night using high-powered lighting. Young-of-the-year char (those less than 50 mm based on size frequency data; Bustard 1999) were not included in the study because it was difficult to distinguish Dolly Varden from bull trout based on physical appearance alone and because areas of sympatry do not correspond with those for older juveniles (Redenbach 2000).

We conducted stomach content analysis on the entire preserved sample. Intact prey items removed from the fish stomachs were identified, counted, and measured by using a dissecting microscope connected through a digitizing tablet to a computer. We also measured mouth width and gill raker spacing because Wankowski (1979) has suggested that these are morphological constraints that salmonids can manipulate that influence the size range of prey. We obtained the total biomass of intact prey items for each stomach by weighing the gut contents after they had been dried in a dessicator, and regular measurements indicated that the weights had stabilized (typically after 2 days).

Density compensation

Density compensation between the species was investigated for all 4 years (1995–1998) of the population-monitoring surveys (Bustard 1999). Fieldwork was conducted during August across 22 sites for which multiple years of data exist. We sampled fish populations by the two-pass removal method (Seber and LeCren 1967) using electrofishing equipment at sites completely enclosed by stopnets. Sites included the entire wetted channel unless flow characteristics did not allow this, in which case an area enclosed along the stream margin was used. All fish captured were anaesthetized, identified to species, measured, weighed, and then released. At sites for which aging and molecular genetic analyses were planned, scales and tissue samples were also taken.

Statistical analyses

In strict sympatry of the tributary stream environment, resource-use traits for both species were generally positively related to body size and lognormally distributed, which is typical for allometric data (Harvey 1982). We adjusted for the effect of body size differences by collecting samples of both species from across an overlapping size range. We removed the affect of body size differences statistically using analysis of covariance (ANCOVA) on log-transformed data, which we could apply to resource-use traits with continuous distributions (habitat traits water depth and mean current velocity; food traits drift foraging rate, benthic foraging rate, and mean prey item biomass; and time traits total foraging rate and total gut content biomass). We also used ANCOVA to compare mouth width and gill raker spacing for the species. Hydraulic habitat type data (riffle–pool, main channel – side channel) were in discrete categories, so we tested for differences between species using contingency table χ^2 analysis. Patterns of diet utilization consist of several non-independent variables, which often take extreme distributions that complicate their statistical analysis (e.g., Sevenster and Bouton 1998). Consequently, we limited our interspecific comparisons of average diet proportions of each prey category to using the Schoener (1970) index of proportional overlap, as recommended by Wallace (1981). Adjustment of the significance levels for individual tests, which we conducted using the sequential Bonferroni adjustment, took place for three tables (Rice 1989) of statistical tests corresponding to the niche dimensions habitat, food, and time. The overall Type I error rate for the stream resource-use study was then no greater than 15%, within the 10–15% guidelines for exploratory surveys suggested by Chandler (1995).

We tested for interspecific differences in mean of adult body size using Mann–Whitney U tests owing to the small sample sizes for Dolly Varden and hybrid adults. Differences in spawning site depth, spawning site current velocity, and spawning site substrate size were assessed using two-sample t tests. Significance levels were adjusted for multiple comparisons using the sequential Bonferroni adjustment.

For our density compensation analysis, we considered the proper replicate for comparison to be the average for each stream reach of all site densities averaged over all of the years. This was because the individual sites and years were not independent, potentially belonging to the same population. We calculated the regression of the average reach densities of each species on that of the other species using the ordinary least squares technique with untransformed data, which enabled us to compare the resulting slope with null hypotheses slopes of zero (i.e., density of one species is independent of density of the other) and –1 (i.e., complete density compensation) using t tests. Mean total densities of sympatric and allopatric reaches were compared using the two-sample t test.

Results

Life history

Sixteen char, ranging in length from 199 mm to 850 mm, were captured in Thutade Lake from approximately 80 h of tangle-netting effort in both near-shore and open-water habitats. Through molecular analysis, all char were identified as bull trout, consistent with the hypothesis that bull trout undergo a niche shift to the lake that Dolly Varden do not. Of the 12 bull trout for which sex could be determined, eight were female and four were male. Piscivory was also indicated for bull trout in the lake; two mountain whitefish of 132 mm and 123 mm were recovered from the stomach of a 410-mm bull trout, and kokanee salmon (*Oncorhynchus nerka*) of 197 mm and 184 mm were recovered from bull trout of 800 mm and 600 mm, respectively. All other char stomachs were empty, although the stomachs of three bull trout of fork length <230 mm were not sampled.

The two species were different in their reproductive biology (Table 1). The most obvious distinction was a large difference in body size at maturity ($U_{0.05,3,12} = 408$, $P < 0.001$). Mature Dolly Varden (six females and six males) ranged from 113 to 235 mm fork length, averaging 148 mm (N = 12, standard error (SE) = 11 mm), whereas mature bull trout (15 males and 19 females) ranged in size from 440 to 890 mm and averaged 741 mm (N = 34, SE = 16 mm).

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Table 1. Interspecific comparisons of reproductive biology of Dolly Varden and bull trout in sympatry.

	Dolly Varden		Bull trout		
Life-history attribute	Mean	SE	Mean	SE	
Adult fork length (mm)	148 (n = 12)	10.9	740 (n = 34)	15.7	**<0.001**
Spawning site depth (mm)	9.3 (n = 30)	0.9	34.7 (n = 28)	2.2	**<0.001**
Spawning site current velocity (cm·s^{-1})	20.7 (n = 30)	1.5	36.8 (n = 28)	2.5	**<0.001**
Spawning site substrate material D_{50}* (cm)	1.6 (n = 30)	0.1	4.9 (n = 28)	0.3	**<0.001**
Spawning period**	03 Sept. to 08 Oct.	22 Aug. to 12 Sept.	na		

Note: Means were compared with the two-sample t test or the Mann–Whitney U test (fork length). *, defined in methods; **, from incidental observations of spawning behaviour in addition to surveys of spawning areas; na, not applicable.

Three of the larger adult migrants were diagnosed using molecular markers as Dolly Varden – bull trout hybrids and they were intermediate in body size at maturity and averaged 403 mm (SE = 33 mm). These differences were statistically significant in both directions (Dolly Varden versus hybrid, $U_{0.05,3,12}$ = 36, P = 0.005; bull trout versus hybrid, $U_{0.05,3,12}$ = 101, P = 0.001). No precocious, stream-resident bull trout have ever been identified during snorkel surveys of spawning areas or during juvenile population assessment, which has typically taken place immediately before the onset of spawning.

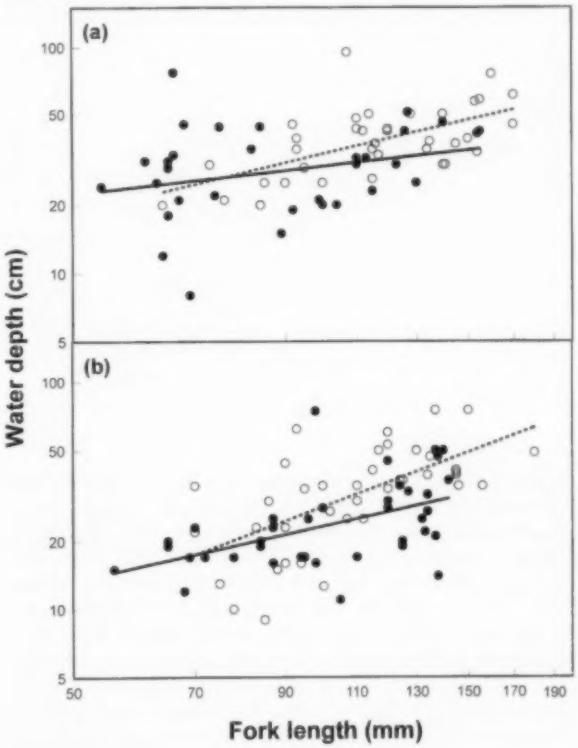
Spawning sites for the two species differed significantly in terms of their physical characteristics (Table 1). Bull trout spawned in deeper water than did Dolly Varden (34.7 cm versus 9.3 cm; $t_{0.05(2),56}$ = 10.80, P < 0.001) and at sites with higher current velocities (36.8 cm·s^{-1} versus 20.7 cm·s^{-1}; $t_{0.05(2),56}$ = 5.51, P < 0.001). The bull trout sites were also found in much larger bed material (D_{50} = 4.9 cm versus 1.6 cm: $t_{0.05(2),56}$ = 12.59, P < 0.001).

Bull trout spawned earlier; the maximum range of spawning activity observed was from August 22 to September 12 compared with September 3 to October 8 for Dolly Varden (Table 1). The spatial distributions of spawning sites also showed little overlap. Within the North Kemess watershed, virtually all Dolly Varden spawning was limited to the reach comprised of the top 4.0 km of North Kemess Creek and the small, mostly seepage fed tributaries that enter this stream section. No bull trout were observed to enter or spawn in the seepage tributaries that are the most important spawning habitats for Dolly Varden, and in most years, very few (<10) spawned in the section of the main stem of Kemess Creek used by Dolly Varden.

Habitat use in tributary streams

Co-existing Dolly Varden and juvenile bull trout in the tributary streams could be distinguished statistically in terms of their resource use, but the differences were subtle. The comparison of focal point water depths (Fig. 2) between Dolly Varden and bull trout was not significant for the daytime observation period (F = 1.99, P = 0.16). The nighttime difference was greater; Dolly Varden were found in deeper water (F = 6.91, P = 0.010, adjusted α = 0.013). The interspecific comparison of daytime mean focal point current velocity revealed different relationship slopes for the two species (Fig. 3*a*). Dolly Varden showed a greater difference relative to bull trout between small and large body size categories (slopes; F = 6.32, P = 0.014, adjusted α = 0.015). Both Dolly Varden (DV) and bull trout (BT) were found at locations of reduced current velocity at night, and the interspecific comparison (Fig. 3*b*) revealed no significant difference (F = 2.83, P = 0.097). All fish observed were closely associated with the stream bottom. The two species used the hydraulic habitat categories (pool, riffle, side-channel pool, and side-channel riffle) in similar proportions, both during the day (χ^2 = 5.76, P > 0.10, BT N = 32, DV N = 37) and night (χ^2 = 3.10, P > 0.25, BT N = 40, DV N = 39) observation periods.

Fig. 2. Interspecific comparisons stream depth at focal point versus fork length (log scale) during (*a*) daytime (F = 1.99, P = 0.16) and (*b*) nighttime (F = 6.91, P = 0.010, adjusted α = 0.013) for sympatric bull trout (solid circles and solid line; daytime N = 32, nighttime N = 40) and Dolly Varden (open circles and broken line; daytime N = 37, nighttime N = 39). See Appendix 1 for relationship equations.



Foraging and diets in tributary streams

Dolly Varden and juvenile bull trout were more distinguishable with respect to the food resource dimensions. During the day, foraging from the drift was more important than

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Fig. 3. Interspecific comparisons of mean current velocity at focal point versus fork length (log scale) during (*a*) daytime (slopes: $F = 6.32$, $P = 0.014$) and (*b*) nighttime (slopes: $F = 2.83$, $P = 0.097$) for sympatric bull trout (solid circles and solid line; daytime $N = 32$, nighttime $N = 40$) and Dolly Varden (open circles and broken line; daytime $N = 37$, nighttime $N = 39$). See Appendix 1 for relationship equations.

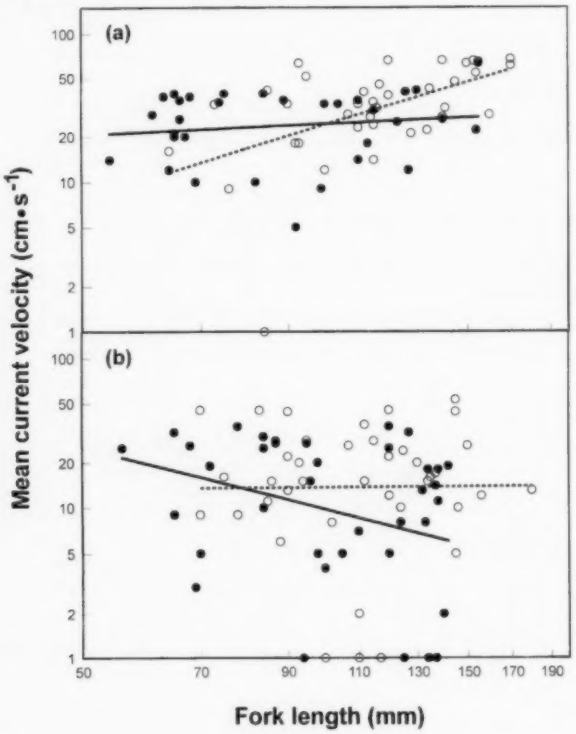
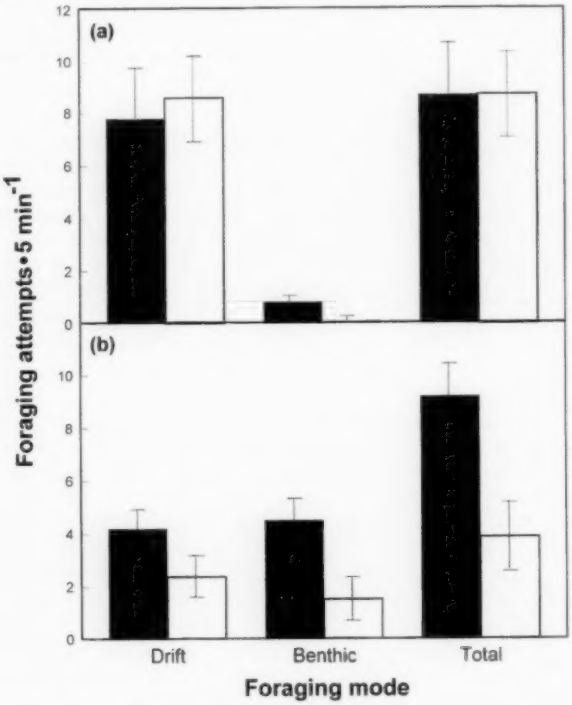


Fig. 4. Observations of foraging mode during (*a*) daytime and (*b*) nighttime for sympatric bull trout (solid bars; daytime $N = 18$, nighttime $N = 26$) and Dolly Varden (open bars; daytime $N = 24$, nighttime $N = 24$). See Appendix 1 for relationship equations. Figures show adjusted means, but interspecific comparisons were made by the analysis of covariance technique (see Results). Error bars are ± standard errors of adjusted means.



benthic foraging for both species (Fig. 4), but the relative importance of benthic foraging increased at night. Interspecific comparison, however, revealed that benthic foraging was more important for bull trout than for Dolly Varden, during both daytime ($F = 7.82$, $P = 0.008$, adjusted $\alpha = 0.01$) and nighttime ($F = 6.72$, $P = 0.010$, adjusted $\alpha = 0.013$) observation periods. Dolly Varden had a slightly higher drift foraging rate by day ($F = 3.65$, $P = 0.062$). Conversely, at night, the bull trout drift foraging rate was higher. This difference was pronounced only for larger individuals, resulting in a difference in the relationship slopes that was not significant ($F = 5.01$, $P = 0.031$, adjusted $\alpha = 0.015$), however, after the correction for the multiple tests. Surface foraging was not important to either species during the period of the study, and thus this category was dropped from the analysis.

Daytime overall foraging rates (Fig. 4) for the two species were very similar ($F = 0.12$, $P = 0.73$), but the nighttime rates were significantly different ($F = 8.77$, $P = 0.0048$, adjusted $\alpha = 0.008$). Dolly Varden expressed a nighttime reduction in overall foraging rate relative to bull trout. The difference in diel foraging patterns, however, was not accompanied by a similar difference in stomach fullness indices between the species (day, $F = 1.31$, $P = 0.26$; night, $F = 0.10$, $P = 0.76$).

Stomach content analysis also revealed interspecific differences, chiefly that juvenile bull trout consumed larger prey items (Fig. 5) than did Dolly Varden ($F = 5.89$, $P = 0.015$, adjusted $\alpha = 0.015$). For the daytime stomach samples, the taxonomic composition of the average Dolly Varden diet was different from that of the bull trout (Fig. 6), having much higher proportions of winged insects. Adult dipterans and hymenopterans made up 33.6% and 7.5%, respectively, of the Dolly Varden diet, compared with 11.3% and 0.6%, respectively, of the bull trout diet. The value of the Schoener (1970) index of proportional overlap between species, however, was 0.71, which implies significant overlap by exceeding the commonly used "biological significance" level of 0.60 (Wallace 1981). Average diet proportions at night were more similar still, with the value of the Schoener index being 0.89 (data not shown).

Juvenile bull trout had relatively larger mouths than Dolly Varden (slopes, $F = 4.8$, $P = 0.03$) and wider gill-raker spacing (slopes, $F = 7.14$, $P = 0.009$), consistent with the finding of relatively larger prey in bull trout diets. Even though the slope differences precluded testing differences in these measures using the analysis of covariance, the separation between them was clear (Fig. 7).

Density compensation

We investigated the effects of the two species' densities

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Fig. 5. Interspecific comparison of average prey item biomass versus fork length (log scale) (F = 5.89, P = 0.015, adjusted α = 0.015) for sympatric bull trout (solid circles and solid line; N = 49) and Dolly Varden (open circles and broken line; N = 39). See Appendix 1 for relationship equations.

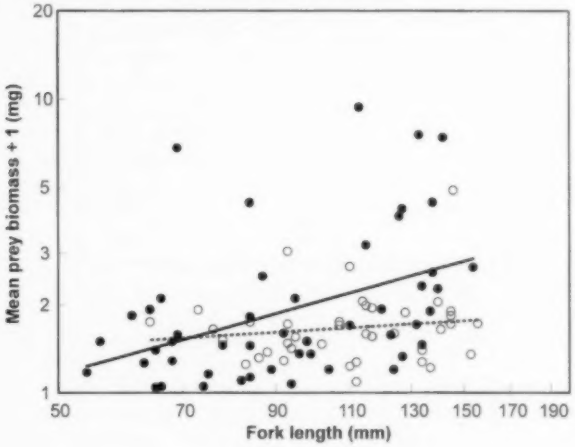
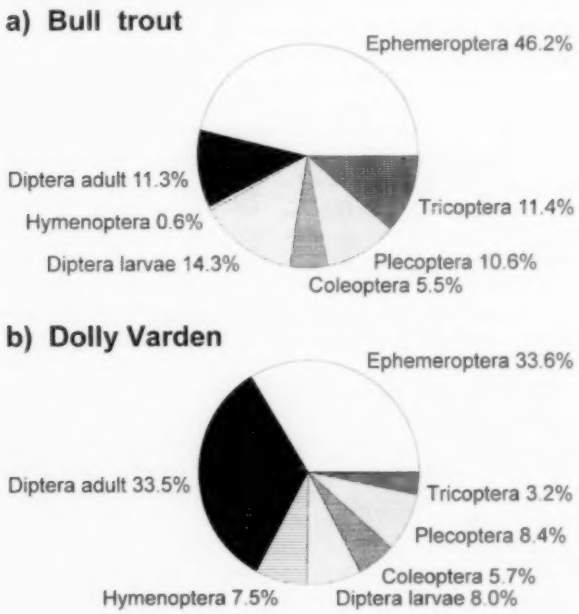
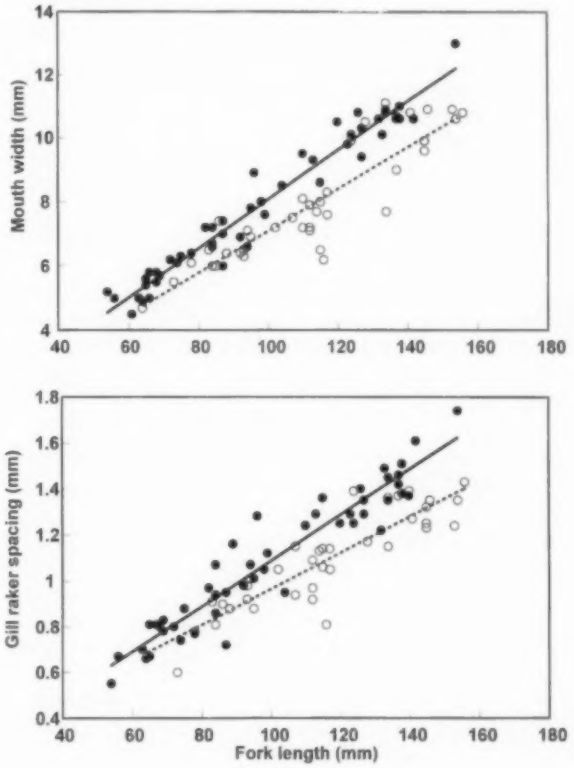


Fig. 6. Interspecific comparison of taxonomic composition of daytime stomach contents (Schoener index of proportional overlap = 0.71) for sympatric (*a*) bull trout (N = 24) and (*b*) Dolly Varden (N = 21).



on each other in sympatry and local allopatry using data from seven reaches that we considered to be independent (Table 2, N = 21 sites total). All were sections of small- to medium-sized tributaries of either Thutade Lake or two larger rivers that drain into the lake (Table 2). Site areas ranged from 55.5 m^2 to 291.2 m^2, averaging 148.3 m^2 (SE = 15.7 m^2).

Fig. 7. Interspecific comparisons of trophic morphology for sympatric bull trout (solid circles and solid line; N = 49) and Dolly Varden (open circles and broken line; N = 37) in terms of (*a*) mouth width (slopes: F = 4.8, P = 0.03) and (*b*) gill-raker spacing (slopes: F = 7.14, P = 0.009). See Appendix 1 for relationship equations.



We found a linear and significant negative relationship between the densities of the two species ($t_{0.05(1),6}$ = 2.79, P < 0.025, r^2 = 0.61, Fig. 8). Further, we found no significant difference between the observed slope (β = –0.94) and that predicted by complete density compensation (Fig. 8, β_0 = –1.0, $t_{0.05(1),6}$ = 0.19, P > 0.50). The average total density of the four sympatric reaches (11.43 fish 100·m^{-2}) was not significantly different ($t_{0.05(2),6}$ = 0.32, P > 0.50) from that of the three allopatric reaches (12.99 fish·100 m^{-2}).

Discussion

Adaptation to different resource environments

In Thutade Lake's tributary streams, the resource environments of Dolly Varden and juvenile bull trout in strict sympatry could be distinguished statistically, but the differences were subtle. Because the distributions of all the resource-use variables showed extensive interspecific overlap with no evidence of discrete niches, there is little indication that Dolly Varden and juvenile bull trout are adapted to divergent resource environments within the tributary streams. Consequently, our data suggest no obvious basis for natural selection against intermediate, hybrid phenotypes during the stream-resident phase of their life history.

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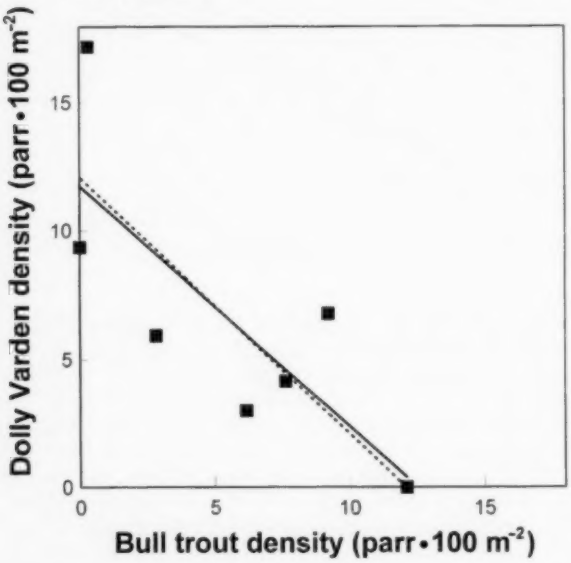
Table 2. Thutade Lake tributary reaches used in analysis of density compensation of one species for missing individuals of the other species (by ordinary least squares regression).

Reach	Category	No. of sites in reach	Average reach densities 1995–1998		
			Bull trout (BT) (100 m^{-2})	Dolly Varden (DV) (100 m^{-2})	Total (100 m^{-2})
North Kemess Creek	Sympatry	4	9.22	6.78	16.00
Upper North Kemess Creek	Allopatry DV	2	0.31	17.20	17.51
Kemess Creek	Sympatry	7	7.64	4.16	11.80
Upper Attichika River	Allopatry BT	1	12.12	0.00	12.12
Tributary 4	Sympatry	3	6.18	2.98	9.16
South Pass Creek	Sympatry	2	2.83	5.93	8.76
Attycelley Creek	Allopatry DV	2	0.00	9.35	9.35
Attichika River (outlier)	Sympatry	1	2.98*	1.95*	2.46*
Niven River (outlier)	Sympatry	5	0.70*	1.13*	0.91*

*Reaches of larger main stems, considered as outliers (see text for explanation).

Fig. 8. Density compensation within independent stream reaches of the Thutade Lake watershed, British Columbia. The slope of the regression of observed Dolly Varden densities on bull trout densities (solid line; $N = 7$, $r^2 = 0.61$, $\beta = -0.94$) was significantly different from the null hypothesis slope of zero ($t = 2.79$, $P < 0.025$) but was not different statistically from the null hypothesis slope of −1 (complete density compensation, broken line; $t = 0.19$, $P > 0.50$).



Pacific basin salmon and trout (*Oncorhynchus* spp.) typically partition resources in streams with respect to microhabitat categories riffle versus pool (e.g., Taylor 1991), depth and velocity (e.g., Everest and Chapman 1972), diet and feeding behaviour (Johnson and Ringler 1980; Nakano and Kaeriyama 1995), and diel feeding periodicity (Johnson and Johnson 1981). Relative to *Oncorhynchus* spp., both Dolly Varden and bull trout are more closely associated with the stream bottom in terms of feeding behaviour, diet, and foraging microhabitat (e.g., Dolloff and Reeves 1990; Nakano et al. 1992). Similar microhabitat utilization occurs for Dolly Varden in the presence of a congener, the Asian white-spotted char (*Salvelinus leucomaenis*), in Japanese watersheds. The more aggressive *S. leucomaenis* feed almost exclusively from the drift, hold midwater focal points, and dominate Dolly Varden of the same size (Fausch et al. 1997). In sympatry with westslope cutthroat trout (*Oncorhynchus clarki lewisi*), bull trout are also strongly associated with a benthic foraging mode and habitat use (Nakano et al. 1992). In our investigation, then, it is perhaps not surprising that both Dolly Varden and juvenile bull trout in the tributary streams were nonaggressive and closely associated with the bottom—this is the feeding niche in which they have been observed during the above studies in allopatry. We did record higher drift foraging rates for both species than are known from these previous studies, but we suspect that the swift current of the steep mountain streams of the Thutade watershed may favour this more stationary foraging mode. The surprising limited resource partitioning by sympatric Dolly Varden and juvenile bull trout may be the result of any one of the following: historical factors either in terms of phylogenetic constraints owing to similar phenotypes or a lack of time since secondary contact for adaptation in sympatry to evolve; a lack of alternative ecological niches in the steep mountain streams of the Thutade Lake watershed; or natural selection for alternative niches that is weak during the juvenile stream-resident phase of char life history.

By contrast, when the entire life history of Thutade Lake watershed char is considered, it is clear that Dolly Varden and bull trout are exposed to very different resource environments for a portion of their lives—bull trout migrate from the tributary streams to Thutade Lake and become piscivorous, whereas Dolly Varden do not. In the lake, bull trout are exposed to a different predation regime, different food resources (primarily fishes compared with insects in the streams), and potential interspecific competition from rainbow trout, which were absent or rare in our tributary stream study sites. In fact, the major morphological characteristics used in species diagnoses of Dolly Varden and bull trout (bull trout have more branchiostegal rays, broader heads, and longer upper jaws) probably reflect adaptation to distinct "piscivore specialist" (bull trout) and "generalist" (Dolly Varden) feeding niches (Cavender 1978). These general ecomorphological and life-history differences have been ob-

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served in other areas of sympatry (McPhail and Taylor 1995; Bustard et al. 1999). Mouth size and gill-raker spacing set limits to the maximum and minimum size, respectively, of prey that salmonids can handle (Wankowski 1979). It appears, therefore, that the larger mouths and greater gill-raker spacing for bull trout recorded in this study are consistent with the idea that they are better adapted to exploit larger-bodied prey in lake or large river habitats and that Dolly Varden are better adapted to exploit the predominantly smaller-bodied prey in stream environments. Consequently, interspecific hybrids that are intermediate in morphology may be at a selective disadvantage when exploiting parental trophic niches (reviewed by Arnold and Hodges 1995).

Constraints to gene flow between species

The different resource environments that Dolly Varden and bull trout experience in the Thutade Lake watershed over their entire life cycle may contribute to constraining gene flow between the species in sympatry. The evolution of postmating isolation as a result of divergent natural selection has been demonstrated convincingly only in the laboratory (reviewed in Rice and Hostert (1993)). Results from field observations and experiments using other taxa, however, offer support for the hypothesis that the intermediate phenotypes of interspecific hybrids may be at a fitness disadvantage in parental niches (e.g., Arnold and Hodges 1995). The discontinuous nature of the Thutade watershed (lake and stream environments) may result in selection against hybrid genotypes and contribute to both pre- and post-mating isolation. First, the survival of hybrids in either lake or stream environments is unknown, but the smaller body size of the hybrids that had spent time in Thutade Lake observed in our study does suggest that hybrids, which are also intermediate in morphology (Haas and McPhail 1991), may be less proficient at exploiting the lake's larger-bodied prey fish resources.

Second, the adaptation of Dolly Varden and bull trout in the Thutade watershed to different life histories also provides a potential mechanism for strong premating isolation between the species. In salmonid taxa, individuals of both sexes typically select mates based on body size (e.g., Jonsson and Hindar 1982; Foote 1988). In the Thutade Lake watershed, then, the difference in body size alone between Dolly Varden and bull trout may promote assortative mating between species. The striking segregation of Dolly Varden and bull trout in terms of physical habitats for spawning is associated with large differences in body size at maturity and, therefore, provides an additional link between life-history differences and premating reproductive isolation. Spawning timing differences are likely important also. Potential causes of the timing differences include differing water-quality characteristics at suitable spawning sites and different egg sizes associated with female body sizes, although these have not been investigated directly. Premating isolation between Dolly Varden and bull trout is not completely effective, however, as evidenced by hybridization across a broad geographic range (Baxter et al. 1997; Taylor et al. 2001). The mechanism by which this gene flow occurs may be "sneak" spawning of the much smaller Dolly Varden males with bull trout pairs, a behaviour that has been documented for other salmonids (Maekawa and Onozato 1986; Wood and Foote 1996) and is consistent with genetic evidence (bull trout mitochondrial DNA introgression into Dolly Varden (Taylor et al. 2001)).

Strong theoretical and experimental support exists for the idea that premating isolation can evolve or be maintained as a consequence of adaptation (e.g., Rice and Hostert 1993; Bush 1994), but specific conditions are required: divergent selection for alternative resource environments is strong relative to gene flow (in sympatry only) and the characters that are the focus of selection in alternative environments cause premating isolation themselves or else are strongly linked to other characters that do. One potential way in which resource exploitation may be linked to reproductive isolation is habitat-specific mating whereby mate choice takes place on or within a preferred habitat or host (Bush 1994). Assortative mating without habitat-specific mating can occur if the characters that reflect specializations to different resource environments also form the basis of premating isolation. For instance, in species pairs of threespine sticklebacks (*Gasterosteus aculeatus*) and in sockeye salmon (*Oncorhynchus nerka*) and kokanee, assortative mating is largely based on a considerable difference in adult body size between sympatric pairs. These are linked to the exploitation of zooplankton in open-water environments or macroinvertebrates in littoral areas by limnetic and benthic sticklebacks, respectively, and the anadromous (sockeye) and non-anadromous (kokanee) life histories (reviewed in Taylor 1999). These examples suggest that the link between body size and sexual selection may be important in promoting or maintaining reproductive isolation when ecological specialization leads to large body size differences. This linkage may, therefore, also contribute to reproductive isolation at the adult life-history stage in Dolly Varden and bull trout, which exhibit similar differences in size at maturity. Finally, although we observed few adult hybrids ($N = 3$), they were intermediate in body size to Dolly Varden and bull trout. Size-dependent spawning site selection in Dolly Varden and bull trout coupled with size-assortative mating behaviour in salmonids raises the hypothesis that natural and sexual selection, respectively, against intermediate-sized hybrid genotypes could also contribute to genetic distinction between sympatric char in spite of gene flow.

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Appendix 1. Regression equations for relationships between log-transformed resource-use variables and $\log_{10}$ body size and between measures of trophic morphology and body size. Interspecific comparisons of relationships were made via analysis of covariance (see Results). Where indicated, D represents daytime and N represents nighttime.

	Regression equations	
Dependent variable	Dolly Varden	Bull trout
Log depth at focal point (cm), D	$Y = 0.85X + 0.67$, $r^2 = 0.35$	$Y = 0.40X + 4.70$, $r^2 = 0.07$
Log depth at focal point (cm), N	$Y = 1.36X + 0.06$, $r^2 = 0.41$	$Y = 0.80X + 0.58$, $r^2 = 0.26$
Log velocity at focal point ($cm \cdot s^{-1}$), D	$Y = 1.63X + 0.01$, $r^2 = 0.26$	$Y = 0.24X + 8.05$, $r^2 = 0.02$
Log velocity at focal point ($cm \cdot s^{-1}$), N	$Y = 0.03X + 11.88$, $r^2 < 0.01$	$Y = -1.37X + 54.22$, $r^2 = 0.10$
Log drift foraging (attempts·5 min^{-1}), D	$Y = -0.40X + 48.0$, $r^2 = 0.02$	$Y = 1.66X + 0.002$, $r^2 = 0.31$
Log drift foraging (attempts·5 min^{-1}), N	$Y = 1.07X + 0.02$, $r^2 = 0.09$	$Y = 2.02X + 0.00032$, $r^2 = 0.31$
Log benthic foraging (attempts·5 min^{-1}), D	$Y = 0.22X + 0.38$, $r^2 = 0.05$	$Y = -0.042X + 1.92$, $r^2 < 0.01$
Log benthic foraging (attempts·5 min^{-1}), N	$Y = 0.16X + 0.83$, $r^2 < 0.01$	$Y = 1.83X + 0.001$, $r^2 = 0.18$
Log total foraging (attempts·5 min^{-1}), D	$Y = -0.23X + 21.80$, $r^2 < 0.01$	$Y = 1.36X + 0.01$, $r^2 = 0.25$
Log total foraging (attempts·5 min^{-1}), N	$Y = 1.14X + 0.014$, $r^2 = 0.08$	$Y = 0.28X + 0.002$, $r^2 = 0.26$
Log stomach content biomass (mg), D	$Y = 2.43X + 0.00$, $r^2 = 0.26$	$Y = 3.45X + 0.00$, $r^2 = 0.30$
Log stomach content biomass (mg), N	$Y = 2.17X + 0.0002$, $r^2 = 0.19$	$Y = 2.31X + 0.001$, $r^2 = 0.22$
Log mean prey item biomass (mg)	$Y = 0.18X + 0.72$, $r^2 = 0.02$	$Y = 0.81X + 0.05$, $r^2 = 0.18$
Mouth size (mm)	$Y = 0.065X + 0.58$, $r^2 = 0.81$	$Y = 0.077X + 0.42$, $r^2 = 0.96$
Gill-raker spacing (mm)	$Y = 0.0078X + 0.18$, $r^2 = 0.80$	$Y = 0.01X + 0.09$, $r^2 = 0.91$

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Climate change and abundance cycles of two sympatric populations of smelt (*Osmerus mordax*) in the middle estuary of the St. Lawrence River, Canada[1]

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Abstract: Commercial catches of two ecologically distinct sympatric smelt (*Osmerus mordax*) populations segregated along the two shores of the St. Lawrence middle estuary exhibited inverse patterns with periodicities on the order of 30 years. The influence of water level in the St. Lawrence River and air temperature, chosen to reflect variations in hydrology and climate, differed markedly between the two populations. Analyses revealed that both water level and temperature were generally positively related with north-shore smelt landings and negatively related with south-shore smelt landings. For both populations, a number of significant climatic factors contributing to variance in smelt landings were lagged by one to three years relative to the year of landings, indicating that climatic variables influenced smelt recruitment. The contrasting role of hydroclimatic variables in driving these abundance cycles is likely related to differential exploitation of estuarine habitats; the south-shore population is associated with shallow shoal habitat, whereas the north-shore population is associated with deep channel habitat. The responses of the two smelt populations also reflect the fundamental ecological differences existing between shoal and channel habitats, indicating that future climate change may differentially affect other populations or species that are segregated between these two habitats.

Résumé : Les débarquements commerciaux de deux populations d'éperlans (*Osmerus mordax*) arc-en-ciel sympatriques, distinctes du point de vue écologique et ségréguées le long des deux rives de l'estuaire moyen du Saint-Laurent, montrent des variations cycliques inverses et une périodicité de l'ordre de 30 ans. L'influence du niveau d'eau du fleuve et de la température de l'air, choisis dans l'étude pour refléter les variations du régime hydrologique et du climat, diffèrent de façon marquée pour les deux populations. Les analyses révèlent que le niveau de l'eau et la température sont généralement corrélés positivement aux débarquements de la rive nord et négativement à ceux de la rive sud. Quelques un des principaux facteurs climatiques contribuant pour une grande part aux variations des débarquements des deux rives étaient décalés dans le temps, indiquant que les facteurs climatiques influencent le recrutement des éperlans. L'effet contrasté des variables hydroclimatiques sur les cycles d'abondance est vraisemblablement liée à l'utilisation différentielle des habitats de l'estuaire; la population de la rive sud est associée à un habitat peu profond et celle de la rive nord est à un chenal profond. Les réponses de ces deux populations d'éperlans reflètent aussi des différences écologiques existant entre des habitats peu profonds et un chenal profond, indiquant que les changements climatiques futurs pourraient avoir des effets différents sur d'autres populations ou d'autres espèces, qui sont ségréguées entre ces deux types d'habitats.

Introduction

Many fish families contain morphologically, ecologically, and genetically distinct populations that are sympatric during at least some part of their life cycle (Taylor 1999). The persistence of sympatric populations is often associated with ecological isolation and the development of ecotypes occupying different habitats in response to disruptive selection (e.g., benthic vs. pelagic morphotypes; McPhail 1984). The development and maintenance of sympatric populations associated with the differential exploitation of a resource gradient may be strongly influenced by the relative abundance of each population (Bridle and Jiggins 2000). However, no evidence is presently available to illustrate either the existence or magnitude of differences in the abundance of ecologically differentiated sympatric populations mediated

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by environmental variation. Long-term variation in climate has been shown to exert considerable influence on the abundance cycles of various aquatic species (Summers et al. 1987; Lluch-Belda et al. 1993). It is well known that major commercial fisheries undergo long-term oscillations in abundance that are governed by climatic events (e.g., Austin and Schubel 1976; Klyashtorin 1998). Given the ecological divergence of sympatric populations, changes in environmental conditions caused by climate variation may be expected to influence differentially their respective life cycles and abundances.

The rainbow smelt (*Osmerus mordax*) is found throughout northeastern North America in both fresh- and salt-water habitats (Scott and Crossman 1974). In lakes, they often form sympatric pairs (Taylor and Bentzen 1993). In the St. Lawrence River, smelt forms an important component of the estuarine fish community where its commercial exploitation has been recorded since 1917. Average annual commercial landings between the 1920s and 1980s varied between 40 and 60 metric tons (t). However, by the 1980s, smelt captures declined in relation to destruction of spawning grounds, chemical pollution, and an abandonment of traditional commercial and recreational fishing activity.

Rainbow smelt occurring in the middle estuary of the St. Lawrence River have long been considered as belonging to one stock for management purposes (Guy Trencia, Société de la Faune et des Parcs du Québec, 8400, avenue Sous-le-Vent, Charny, QC G6X 3S9, personal communication). However, mitochondrial DNA analyses have clearly shown that two genetically distinct populations exploit the St. Lawrence middle estuary (Bernatchez and Martin 1996). Moreover, they are spatially segregated: one is associated with the north shore and the other is found along the south shore of the middle estuary. Limited exchanges of adult smelt between the two shores have been documented by various means since the middle of the 20th century. Mark and recapture experiments conducted in the 1940s and 1950s revealed less than 1% mixing of adult smelt between the two shores of the middle estuary (Vladykov and Michaud 1957; Magnin and Beaulieu 1965). Morphometric analyses of adults demonstrated that smelt caught along the north shore were morphologically distinct from smelt captured on south-shore spawning sites (Fréchet et al. 1983). Finally, morphometric and mitochondrial DNA analyses revealed that less than 3% of the smelt caught by the north-shore commercial fishery originate from the south-shore population (Lecomte et al. 1999).

The two populations show considerable ecological divergence and may thus be expected to respond differently to environmental variability. Smelt associated with the south shore spawn in small tributaries just above the limit of salt intrusion (Ouellet and Dodson 1985). Larvae are quickly transported to the middle estuary where they occupy the shallow shoal habitat that characterizes the south shore of the estuary (F. Lecomte and J.J. Dodson, unpublished). In contrast, smelt associated with the north shore spawn ~100 km upstream in the St. Lawrence River freshwater estuary, near Neuville (Fig. 1). Following hatching, larvae drift downstream to the middle estuary. They are retained in the estuarine turbidity maximum by a combination of active vertical tidal migrations and estuarine circulation (Laprise and Dodson 1989). Larvae, juveniles, and adults of this population are mainly associated with the deep waters of the channel habitat that characterize the north shore as well as much of the middle estuary.

We focused on river discharge and temperature as the two environmental variables most likely to influence the abundance of estuarine smelt populations. Discharge plays a pivotal role in the structure and functioning of large river ecosystems (Vincent and Dodson 1999). In the St. Lawrence, discharge influences the abundance cycles of several commercially important species. For example, the year-class strength of lake sturgeon (*Acipenser fulvescens*) is strongly related to discharge in June (Nilo et al. 1997). The reproductive success of tomcod (*Microgadus tomcod*) during the winter also appears to be a function of discharge and tidal state (Fortin et al. 1990). Strong positive correlations were found between halibut and lobster catches in the Gulf of St. Lawrence and the mean discharge of the St. Lawrence River (Sutcliffe 1973). Temperature is also a dominant factor influencing most aspects of food-web processes at many trophic levels. We thus tested the hypothesis that river discharge and temperature play a significant role in controlling the abundance cycles of estuarine smelt populations, as indicated by commercial landings recorded throughout the 20th century. Given the fundamental ecological differences between the two smelt populations at all life history stages, we predicted that the two populations have responded differently to variations in these hydroclimatic factors. Finally, we discuss how these findings influence conservation strategies in the St. Lawrence estuary in the face of future climate change.

Materials and methods

Smelt landings were reported by fishers from 1917 to 1979 and compiled by the Bureau de la Statistique du Québec (Bérubé 1990; Bérubé and Yergeau 1992). These fishers have traditionally used large trap nets equipped with wings and leaders mounted on wooden posts in the littoral zone. They are normally installed every year at the same location early in the spring and removed during the fall. The fishing zones used for the present study extended from Anse-à-Gilles to Trois-Pistoles along the south shore (~200 km) and from Cap Tourmente to the Saguenay River along the north shore (~180 km; Fig. 1). There is no recorded fishing effort between the two shores in the open waters of the middle estuary. The traps are multi-specific, capturing other pelagic fish (including herring and capelin). Only the catches registered along the north and the south shores of the St. Lawrence middle estuary were used in this study and are expressed as total annual catches for each shore. Studies conducted since the middle of the 20th century have consistently shown that the two populations remain spatially segregated in commercial catches along the two shores throughout the ice-free season. We thus assumed that this spatial segregation has been maintained throughout the 20th century and that the landings recorded from trap nets located on either the north or south shore are a reliable indicator of the abundance of each population. Catch statistics from the south shore started in 1917 and from the north shore in 1922. Landings after 1979 are not taken into account due to large-scale abandonment of the smelt fishery related to habitat deterioration (Lecomte et al. 1999; see Discussion).

Aberrant values in the smelt catches, mainly registered during and shortly after World War II, were removed from the series. These outlying values were identified using the extreme studentized deviate method (also called Grubbs test; Grubbs 1969), recommended by the United States Environmental Protection Agency (USEPA 1992), and applied on segments of at least seven

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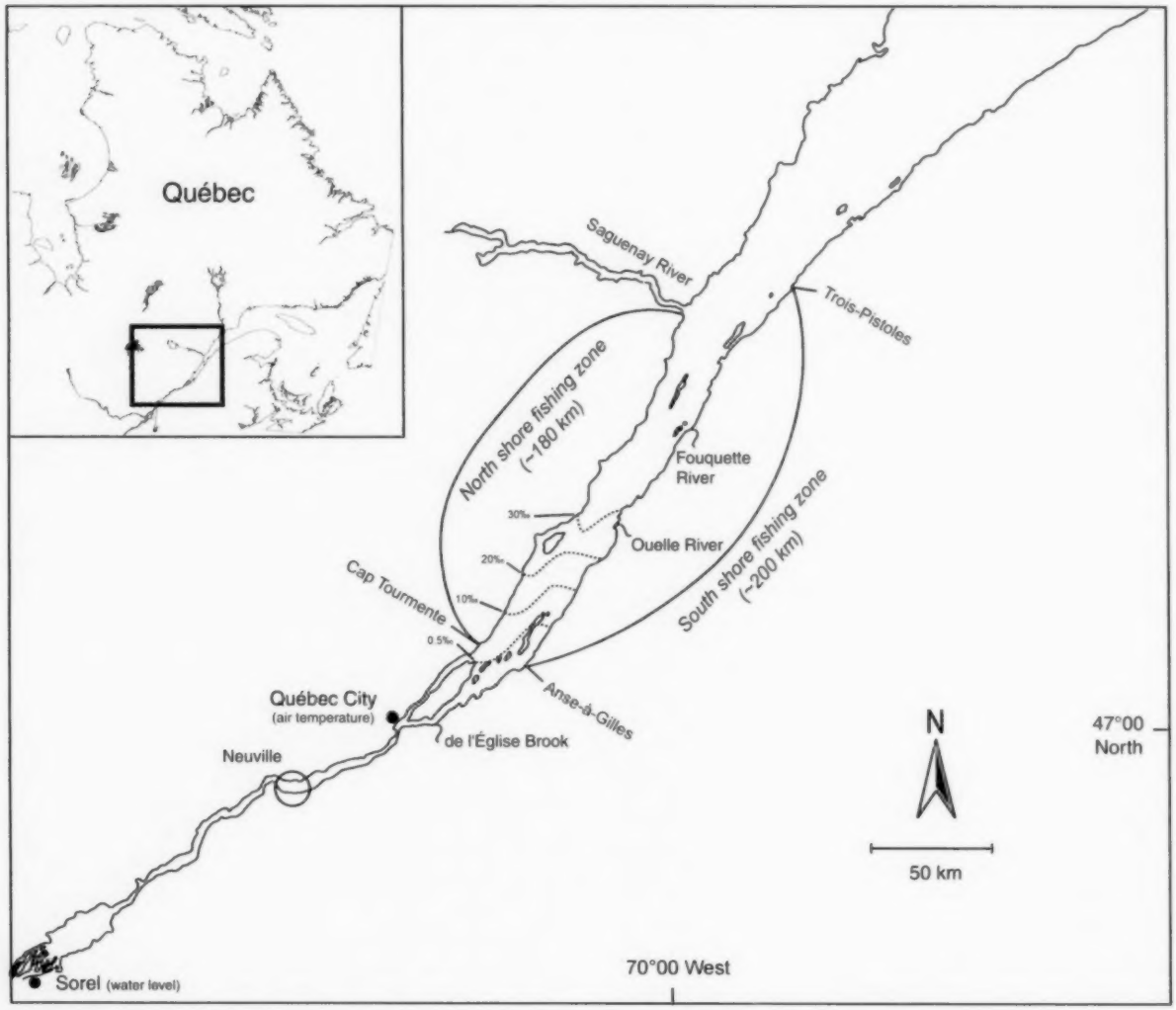
Fig. 1. Study area, location of water level (Sorel) and temperature (Québec City) measurement stations, fishing zones, and average position of isohaline (‰) on the flood tide in the middle estuary of the St. Lawrence River, Canada. Spawning areas of the north-shore smelt population are located near Neuville and those of the south-shore smelt population are found in de l'Église Brook, Fouquette River, and Ouelle River.



values in the data series. The outliers correspond to the years 1941, 1942, 1944, 1947, 1950, and 1960 on the north shore, and to the year 1943 on the south shore. As the time series were relatively short (~60 data points), these missing data points were replaced with modelled values fitted to the raw data (simple exponential smoothing; SAS 1999). The cyclical patterns in both catches and climatic factors were characterized using a single spectrum Fourier analysis.

Because the smelt catches are expressed as annual landings and not as catch per unit effort, observed abundance cycles may partially reflect varying fishing effort or catchability. To test for this possibility, we verified whether the annual catches were correlated with the number of fishers (of smelt, herring, eel, others, and total) and (or) with the annual mean catches of other species captured in the same trap nets in the estuary (herring, capelin, and total catch). These additional variables were also available in the fisheries statistics (Bérubé 1990; Bérubé and Yergeau 1992).

Hydrological measurements came from Hydat, a CDROM updated by Environment Canada (HYDAT 1998). Water levels have been measured at the hydrographic station located at Sorel (Fig. 1) since 1912 and it was chosen as the reference station to represent the St. Lawrence River hydrological regime. Although we would have preferred to use flow rate in the St. Lawrence River, direct measurements are available only in the vicinity of Montréal, upstream of major affluents. Furthermore, flow reconstitution immediately upstream of the middle estuary (Québec City) requires a complex set of calculations and has only been completed for the years 1932 to 1998 (Jean Morin, Meteorological Service of Environment Canada, 1141 route de l'Église, Sainte-Foy, QC G1V 3W5, unpublished data). As the monthly average water levels at Sorel are strongly correlated with the reconstituted discharge data at Québec City ($r = 0.88$ and $p < 0.05$ for monthly means between 1932 and 1998), we used water level at Sorel as a surrogate measure of the river's flow into the middle estuary. Discharge is considered to

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have a far greater influence on smelt population dynamics than differences in water level because of the strong tidal regime in the middle estuary to which smelt populations are consistently exposed (mean tide range at Québec City is 4.1 m, but spring tide range can be as much as 6.9 m at the eastern tip of Île d'Orléans; SLC 1996). The Meteorological Service of Environment Canada also provided daily measurements of air temperature at Québec City in the vicinity of spawning and fishing areas. Water temperatures in the St. Lawrence River near Québec City are available only for the last decade, but are strongly correlated with air temperature (e.g., r = 0.95 and $p < 0.05$ for monthly means between 1986 and 1997). The daily measurements of water levels and temperature were used to calculate annual, semi-annual (between April and September to encompass the growing season), and monthly averages between 1917 and 1979. Water levels are expressed in metres according to the International Great Lakes Datum 1985. Two missing data points for water level (one in March and one in April) and one for temperature in August were replaced with the same implementation procedure used for annual smelt catches.

Climatic variables significantly correlated to smelt abundance were identified using univariate cross-correlation analyses (Pearson r; $p < 0.05$). Annual, semi-annual, and monthly averages of water level and air temperatures were computed to isolate specific moments of the year significantly related to annual smelt abundance. A lag of 0, –1, –2, and –3 years was introduced to detect any possible recruitment signal in the data series. Because smelt reproduce at 2–3 years of age and 2–3-year-old smelt dominate the commercial landings (Fournier and Landry 1990), changes in survival of young-of-the-year smelt related to temperature or discharge would not be evident in commercial catches for a period of 2–3 years.

Multiple regressions (forward stepwise; $p < 0.10$) were computed to quantify the relative contribution of significant climatic variables to variation in smelt landings and to rank them in order of importance. We used catches as dependent variables (north and south shores) and a set of significant climatic factors identified in univariate cross-correlation analyses as independent variables. Because the same data set was used in both univariate cross-correlation and multiple regression analyses, the latter cannot be used to reduce the probability of spurious correlations.

To explore the sensitivity of our findings to autocorrelation in the data series, we compared the results of the cross-correlation analyses using the uncorrected data series with that using a "prewhitened" data series. Prewhitening involved fitting the time-series model presented in Pyper and Peterman (1998, eq. 8) to each data set and using the residuals for computing correlations. Another multiple regression analysis was conducted as described above but using the time series of smelt landings and climatic variables corrected for autocorrelation. Except for the Grubbs test (available at www.graphpad.com/www/grubs.htm), the statistical analysis was carried out using Statistica™ edition 1998 (Statsoft Inc.; available at www.statsoft.com) and SAS (1999).

Results

Smelt landings

Low-frequency fluctuations were found in the landings. Smelt catches on the north shore varied with a periodicity of approximately 38 years (Fourier analysis; $p < 0.05$) (Fig. 2). The periodicity observed on the south shore is approximately 31 years (Fourier analysis; $p < 0.05$) (Fig. 2). The long-term patterns of smelt landings on the two shores are inverted resulting in a negative correlation between north- and south-shore landings (r = –0.41 and $p < 0.01$).

Smelt catches were not correlated with the number of smelt fishermen ($p > 0.05$). In addition, no significant correlations were observed between the annual catches of smelt and that of other pelagic fishes in the estuary including herring, capelin, and total fish landings ($p > 0.05$).

Hydroclimatic variables

Low-frequency fluctuations were also found in the climatic factors. Annual mean water levels measured at Sorel varied with a periodicity of approximately 34 years (Fourier analysis; $p < 0.05$) (Fig. 3). The annual mean air temperatures at Québec City varied with a periodicity of about 68 years (Fourier analysis; $p < 0.05$) (Fig. 3). Analyses of semi-annual and monthly means for both water levels and temperatures revealed periodicities similar to those of the annual means (data not shown).

Autocorrelation

The long-term data series of smelt landings contain positive autocorrelations only at lag-1 for the north and south shores. The annual, semi-annual, and monthly mean water levels had a significant autocorrelation at lag-1. No autocorrelation was found in the temperature series.

Univariate cross-correlation analyses

Time series uncorrected for autocorrelation

The two smelt populations differed in their responses to variations in water level. The smelt catches from the south shore of the St. Lawrence estuary are strongly and negatively correlated with the annual mean water levels at Sorel of year 0, to semi-annual mean water levels of year 0 and lagged by one year, and to monthly means between March and July (Table 1). The strongest correlations were found during the spring floods (April) of year 0, with a correlation coefficient r_0 = –0.50 and $p < 0.01$ (Table 1). The strength of the correlations tends to decrease but remains significant when introducing a lag of –1, –2, and –3 years in the analysis (Table 1). In contrast, the correlation coefficients between water level and smelt catches on the north shore are in general positively correlated with annual, semi-annual, and monthly averages. Significantly positive correlations between smelt landings and water levels were observed during March of year –2, April of year –1, and September of year –1. Significantly negative correlations occurred in December of years –2 and –3 (Table 2).

The two smelt populations also varied differently in their responses to variations in temperature. The correlation coefficients between temperature and smelt catches on the north shore are strong, significant, and positive for the annual and semi-annual means and in May of year 0, and tend toward null coefficients for the rest of the year and also when introducing a lag of –1, –2, and –3 years in the analysis (Table 2). In contrast, on the south shore, significant and negative correlations were found with the semi-annual mean temperatures of year 0 and year –1 as well as during August of year 0 and year –1 (Table 1).

Prewhitened time series

When the time series were corrected for autocorrelation (prewhitened), the relative importance of climatic variables on smelt landings along the two shores differed, whereas the sign of the correlations remained the same. On the south

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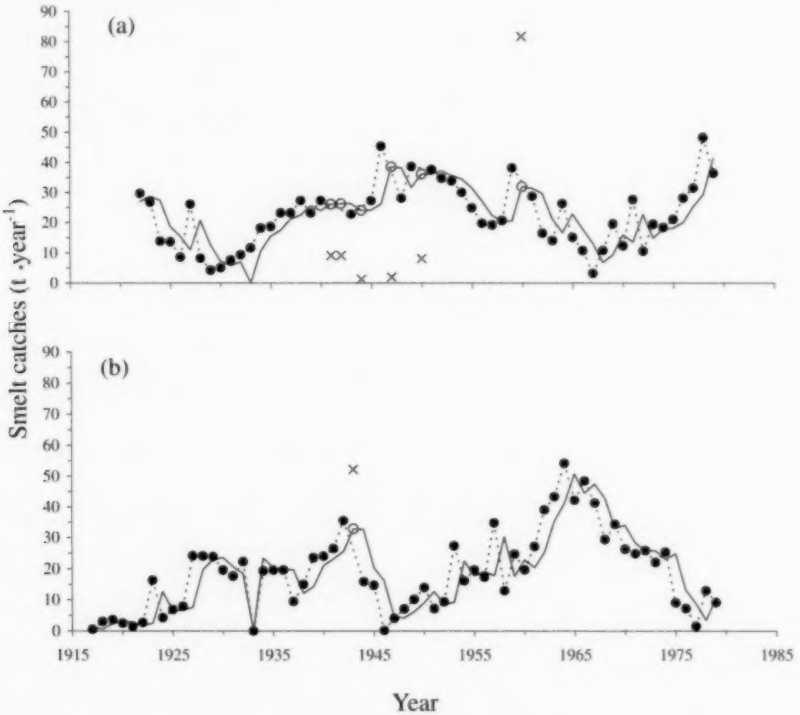
Fig. 2. Total annual smelt landings in tonnes per year ($t \cdot year^{-1}$) in the St. Lawrence middle estuary for (*a*) the north shore (1922–1979) and (*b*) the south shore (1917–1979); the symbol (●) and the broken line correspond to raw annual smelt catches, (×) to outliers removed from the series, and (○) to modelled values fitted to the raw data using a simple exponential smoothing (solid line). The cyclical patterns in both catches and climatic factors were characterized using a single-spectrum Fourier analysis (38 years for the north shore and 31 years for the south shore; $p < 0.05$).



shore, prewhitening reduced the number of significant correlations between water level and smelt landings from 15 to 3. However, the majority of correlations remained negative (37 in the prewhitened series vs. 32 in the uncorrected series of a total of 48 correlations). After prewhitening, smelt landings were significantly correlated to the March water level measured one year prior to landings and to those measured in October and December of the same year as the landings. (Table 1).

Following prewhitening, the four significant correlations observed between smelt landings on the south shore and temperature were no longer significant but remained negative. The majority of correlations were negative before and after prewhitening (38 before and 27 after prewhitening of 48 correlations). Smelt landings were significantly correlated to semi-annual temperature and mean October temperature (lagged by three years) and the December mean temperatures of the same year (Table 1).

On the north shore, mean annual and semi-annual water levels and monthly means between May and October were all significant following prewhitening (except July). The significant correlations observed between landings and December water levels lagged by two and three years were reduced to nonsignificance following prewhitening (Table 2).

The correlation coefficients between temperature and smelt catches on the north shore before and after prewhitening remained essentially the same (Table 2). Following prewhitening, three new significant correlations were added: mean semi-annual temperature lagged by two years, April mean temperature of the same year, and October temperature lagged by three years.

Multiple regression analyses

The most significant climatic factors identified at $p < 0.05$ by the univariate cross-correlation analyses were combined as independent variables in multiple regression analyses, except when climatic variables were recorded after the fishing period in the same year as the landings (i.e., October and December water levels and temperatures, Tables 1 and 2). These were considered spurious correlations, since no plausible mechanisms can explain such relationships. The respective contributions to variance in smelt landings of the significant climatic variables retained for the analysis were quantified (Table 3). Uncorrected and prewhitened time series were analysed separately and compared. The multiple regression model for the south shore based on uncorrected time series combined four significant climatic factors explaining together up to 45% of the variance in smelt catches (Table 3). Mean April water level measured the same year as recorded landings explained 25% of the variance in smelt catches. Mean April water level two years prior to recorded landings explained an additional 10% but was removed at step 5 of the analysis. Mean April water level three years prior to recorded landings explained an additional 5% of the

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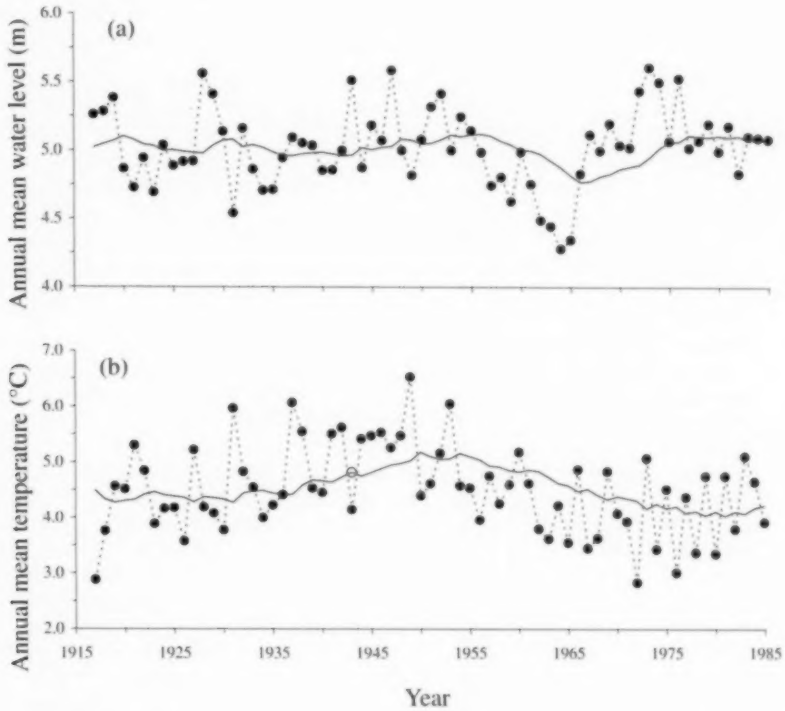
Fig. 3. Annual mean (*a*) water levels measured at Sorel and (*b*) air temperatures at Québec City between 1917 and 1985. The broken line corresponds to raw annual smelt catches and the solid line to a simple exponential smoothing. The water level series shows a periodicity of approximately 34 years and the temperature series varies with a period of about 68 years (single-spectrum Fourier analyses; $p < 0.05$).



smelt catch. Mean March water level measured one year prior to recorded landings explained an additional 4% of the catch. Finally, the semi-annual temperatures averaged between April and September of the same year as recorded landings also explained 3% of the variance in smelt catches (Table 3).

Removing autocorrelation from the time series eliminated the significant negative correlations between spring water level and landings on the south shore (Table 3). For the prewhitened time series, mean October temperature three years before landings (explaining 9% of the landings) and mean March water level one year before landings (explaining 6%) were identified as the most significant climatic variables influencing smelt catches.

The multiple regression model based on the uncorrected time series for the north shore also combined four significant climatic factors explaining together 39% of the variance in smelt catches. Semi-annual temperatures averaged between April and September of the same year as recorded landings explained 15% of the variance in smelt catches (Table 3). Mean water level during March two years prior to recorded landings explained an additional 10% of the smelt catch (Table 3). Finally, mean December water levels measured two and three years prior to recorded landings explained an additional 9% and 5% of the catch (Table 3).

The multiple regression analysis of the prewhitened data series revealed some differences in the relative importance of climatic variables and the lag period. Semi-annual water level lagged by one year explained 14% of the variation in smelt landings. Mean semi-annual temperature lagged by two years explained 8% and mean October temperature lagged by three years explained 7% (Table 3).

Discussion

The time-series analysis of smelt landings and hydroclimatic factors in the St. Lawrence middle estuary revealed that the abundance of both smelt populations fluctuated significantly in relation to air temperature and water level with a periodicity of approximately 30 to 38 years. The periodicity of the cycles is difficult to assess with accuracy as only two cycles are represented in the landings and the water level series and only one cycle is represented in the temperature series. Nevertheless, comparable long-term cycles with periodicities of about 25 years have been reported in Great Lakes and St. Lawrence River water levels (Chanut et al. 1988 and references therein). Most importantly, the long-term patterns in smelt landings on the north and south shores are antiphase cycles. Water level and air temperature, chosen as two variables reflecting long-term changes in hydrology and climate, were significantly correlated with long-term patterns in smelt landings. However, the influence of these hydroclimatic variables differed markedly between the two sympatric populations. Univariate cross-correlation analysis using both uncorrected and prewhitened data series to remove autocorrelation revealed that both hydroclimatic vari-

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Table 1. Pearson's correlation coefficient r for correlations between total annual smelt catches for the south shore (1917–1979) of the St. Lawrence middle estuary and annual, semi-annual, and monthly mean water levels at Sorel and air temperature at Québec City.

	South uncorrected				South prewhitened			
Parameter	0	–1	–2	–3	0	–1	–2	–3
Water level								
Annual	**–0.36***	–0.24	–0.16	0.00	–0.15	–0.05	–0.13	0.02
Semi-annual	**–0.40***	**–0.31***	–0.24	–0.09	–0.11	–0.12	–0.17	–0.04
January	–0.14	–0.06	–0.01	0.10	–0.14	–0.01	–0.06	0.00
February	–0.06	–0.02	0.11	0.13	–0.04	–0.13	0.09	–0.03
March	**–0.46***	**–0.43***	–0.24	–0.24	–0.09	**–0.30***	0.09	–0.12
April	**–0.50***	**–0.43***	**–0.37***	**–0.32***	–0.16	–0.15	–0.05	–0.12
May	**–0.34***	**–0.29***	**–0.28***	–0.11	–0.09	–0.06	–0.23	–0.05
June	**–0.36***	**–0.30***	–0.22	–0.08	–0.08	–0.16	–0.16	–0.10
July	**–0.28***	–0.23	–0.12	0.01	–0.01	–0.17	–0.11	–0.07
August	–0.20	–0.13	–0.01	0.12	–0.06	–0.19	–0.08	0.05
September	–0.18	–0.06	0.02	0.14	–0.22	–0.03	–0.08	0.02
October	–0.16	0.05	0.05	0.19	**–0.33**	0.16	–0.17	0.12
November	–0.03	0.08	0.10	0.24	–0.12	0.09	–0.12	0.15
December	–0.15	0.11	0.12	0.25	**–0.31**	0.10	–0.09	0.14
Temperature								
Annual	–0.15	–0.24	–0.20	–0.14	–0.02	–0.17	–0.10	–0.10
Semi-annual	**–0.28***	**–0.28***	–0.18	–0.20	–0.16	–0.24	0.03	**–0.26***
January	0.07	0.07	–0.06	0.07	0.00	0.18	–0.11	0.18
February	–0.04	–0.12	–0.12	–0.12	0.02	–0.12	0.02	0.06
March	–0.16	–0.05	–0.09	–0.02	–0.18	–0.07	–0.09	–0.04
April	0.03	–0.02	0.05	–0.08	0.05	–0.10	0.18	–0.02
May	–0.11	–0.18	–0.14	–0.20	–0.04	–0.09	0.03	–0.02
June	0.03	–0.06	–0.05	–0.02	0.13	–0.12	0.08	0.10
July	–0.20	–0.19	–0.07	–0.17	–0.07	–0.24	0.08	–0.21
August	**–0.28***	**–0.26***	–0.14	–0.08	–0.10	–0.25	–0.09	–0.07
September	–0.08	–0.01	0.01	–0.01	–0.13	–0.06	0.05	–0.15
October	–0.02	–0.06	–0.10	–0.07	0.04	0.06	–0.12	**–0.30***
November	0.05	–0.01	–0.06	0.02	0.06	0.07	–0.12	0.02
December	0.13	–0.16	–0.14	–0.13	**0.37**	–0.06	–0.13	–0.03

Note: Semi-annual corresponds to the averaged daily values recorded between April 1 and September 30. Correlations were performed with uncorrected and prewhitened time series and with lags of 0, –1, –2, and –3 years. Probability levels $p < 0.05$ are in bold; * corresponds to the variables used in the multiple regression analysis.

ables were generally positively related to north-shore smelt landings and negatively related to south-shore smelt landings.

Correcting the time series of smelt catches and water level for autocorrelation had a contrasting effect on our understanding of the dynamics of the two sympatric populations. For the north-shore population, three of the four significant climatic factors contributing to variance in smelt landings for both the uncorrected and prewhitened data series were lagged relative to the year of landings indicating that climatic variables influence recruitment. The positive influence of either temperature measured during the same year as captures or water level measured one year earlier was manifest at the semi-annual level (April–September), with monthly means of either water levels or temperatures being of secondary importance. For the south-shore population, two of the four significant climatic factors contributing to variance in smelt landings for the uncorrected data series were lagged relative to the year of landings indicating that climatic variables also influence recruitment of south-shore smelt. However, in contrast to the north-shore population, variance in the abundance of the south-shore population seems to be clearly related to water levels occurring in March or April either during the same year as landings or one to three years prior to the year of landings. Unfortunately, removing the effect of autocorrelation also eliminated this relationship. The significance of December temperatures and October water levels observed during the same year as the catches were recorded, thus after the annual closure of the fishery, cannot be interpreted. Although the removal of autocorrelation is statistically justified to compute correlations between two data series, removing autocorrelation also results in removing low-frequency variability from the data (Pyper and Peterman 1998). If the low-frequency components of variability in two time series are synchronous, then removing the autocorrelation may also remove much of this covariance (Thompson and Page 1989). It thus appears that prewhitening the data series eliminated an important relationship between long-term environmental processes and the dynamics of the south-shore smelt population.

Differing long-term fluctuations in abundance between sympatric smelt populations and the contrasting role of hydroclimatic variables in driving these cycles are likely re-

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Table 2. Pearson coefficient r for correlations between total annual smelt catches for the north shore (1922–1979) of the St. Lawrence middle estuary and annual, semi-annual, and monthly mean water levels at Sorel and air temperature at Québec City.

	North uncorrected				North prewhitened			
Parameter	0	–1	–2	–3	0	–1	–2	–3
Water level								
Annual	0.07	0.19	0.06	–0.02	–0.16	**0.33***	–0.02	0.15
Semi-annual	0.09	0.24	0.04	–0.05	–0.14	**0.37***	–0.03	0.18
January	0.09	0.01	0.01	–0.02	0.11	–0.01	0.02	0.05
February	0.05	0.00	0.06	0.01	0.05	–0.06	0.07	0.05
March	0.22	0.12	**0.27***	0.13	0.15	–0.12	0.26	0.08
April	0.21	**0.28***	0.15	0.03	–0.01	0.22	0.09	0.12
May	0.02	0.19	–0.07	–0.18	–0.17	**0.37***	–0.04	0.15
June	0.08	0.19	–0.01	–0.05	–0.09	**0.32***	–0.06	0.18
July	0.03	0.13	–0.01	–0.02	–0.11	0.24	–0.06	0.20
August	0.08	0.23	0.08	0.01	–0.15	**0.35***	–0.01	0.17
September	0.12	**0.27***	0.16	0.04	–0.18	**0.37***	0.05	0.08
October	–0.01	0.21	0.07	0.01	**–0.27**	**0.36***	–0.01	0.08
November	–0.12	0.01	–0.12	–0.03	–0.20	0.24	–0.17	0.01
December	–0.22	–0.17	**–0.29***	**–0.29***	–0.19	0.10	–0.16	–0.10
Temperature								
Annual	**0.38***	0.18	0.23	0.08	**0.33***	–0.01	0.22	–0.09
Semi-annual	**0.39***	0.19	0.26	–0.03	**0.33***	–0.01	**0.36***	–0.06
January	–0.03	–0.08	–0.13	–0.10	0.04	0.00	–0.13	–0.07
February	0.13	0.05	0.17	0.19	0.13	–0.03	0.06	0.10
March	0.12	–0.02	0.10	–0.05	0.19	–0.03	0.14	–0.12
April	0.16	–0.02	0.21	0.10	**0.26***	–0.15	0.15	0.00
May	**0.34***	0.18	0.06	–0.04	**0.27***	0.15	0.13	–0.15
June	–0.08	–0.09	–0.04	–0.05	–0.06	–0.10	–0.03	0.18
July	0.14	0.05	0.02	–0.07	0.16	0.09	0.09	–0.03
August	0.07	0.15	0.08	–0.11	–0.02	0.15	0.18	0.07
September	0.07	–0.14	–0.09	–0.22	0.21	–0.19	0.14	–0.19
October	0.12	–0.02	0.04	–0.11	0.15	–0.10	0.15	**–0.27***
November	0.06	0.17	0.14	0.13	–0.10	0.08	0.09	–0.08
December	0.12	0.08	0.03	0.20	0.03	0.08	–0.10	0.13

Note: Semi-annual corresponds to the averaged daily values recorded between April 1 and September 30. Correlations were performed with uncorrected and prewhitened time series and with lags of 0, –1, –2, and –3 years. Probability levels $p < 0.05$ are in bold; * corresponds to the variables used in the multiple regression analysis.

lated to the differential exploitation of estuarine habitats. The two smelt populations exploit distinct physical habitats at all life stages. In the St. Lawrence middle estuary, the contrasted topography of the two shores drives the local hydrodynamics and influences water temperature. The south shore is characterized by large strands, a smooth slope, and shallow waters (<3 m), contrary to the north shore that corresponds to a deeper bed with a steep lateral slope (~20 m deep within 1 km of shore), high current speeds, and strong three-dimensional mixing processes (Laprise and Dodson 1989). As we have convincing evidence that these two populations are spatially segregated throughout their growing season (Fréchet et al. 1983; Bernatchez and Martin 1996; Lecomte et al. 1999), it is unlikely that the cause of variation in population abundance is the result of intraspecific competition for resources. Rather, it is likely that the south-shore population exploits a benthic feeding niche, whereas the north-shore population exploits a pelagic one. Exploitation of the benthic–pelagic resource gradient characterizes many species pairs (e.g., Smith and Skúlasson 1996).

High smelt landings on the south shore of the St. Lawrence estuary correspond to years of low spring water levels. Water level explains a significant fraction of the variance in the catches from the south shore and corresponds to the magnitude of the spring flood recorded either the same year as the catches, or one or three years before the year the catches were recorded. It is unlikely that water level itself directly influences the survival and recruitment of smelt in the macrotidal middle estuary. The shallow shoals along the south shore are exposed at low tide and flooded at high tide regardless of water level in the St. Lawrence River. It is more likely that discharge and associated current speeds have a greater impact on smelt population abundance. High discharge may influence larval survival in the shallow nursery areas, subsequent recruitment to the adult population, and survival of adults and their prey in the shallow feeding habitats. Newly hatched larvae leave their natal streams in mid-May shortly after hatching and are rapidly transported downstream (Ouellet and Dodson 1985). Young-of-the-year smelt appear to be passively retained in shallow bays along the south shore (F. Lecomte and J.J. Dodson, unpublished data). Because of Coriolis force and estuarine topography,

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Table 3. Results of two multiple regression analyses (forward stepwise selection) between total annual smelt catches of the north and south shores in the St. Lawrence middle estuary and the most significant climatic factors identified by the univariate cross-correlation analyses. The analyses were performed for uncorrected and prewhitened time series.

Step	Variable	Variable removed	Partial R^2	Multiple R^2	F value	p
North shore						
Uncorrected time series						
1	**Semi-annual temperature –0**		**0.15**	**0.15**	**10.19**	**0.002**
3	**Water level March –2**		**0.10**	**0.25**	**8.11**	**0.006**
2	**Water level December –2**		**0.09**	**0.34**	**6.30**	**0.015**
4	**Water level December –3**		**0.05**	**0.39**	**4.24**	**0.045**
Prewhitened time series						
1	**Semi-annual water level –1**		**0.14**	**0.14**	**8.80**	**0.005**
3	**Seasonal temperature –2**		**0.08**	**0.22**	**5.63**	**0.022**
4	**Temperature October –3**		**0.07**	**0.29**	**5.34**	**0.025**
South shore						
Uncorrected time series						
1	**Water level April –0**		**0.25**	**0.25**	**19.77**	**0.000**
2	Water level April –2		0.10	0.35	9.49	0.003
3	**Water level April –3**		**0.05**	**0.40**	**5.10**	**0.028**
4	**Water level March –1**		**0.04**	**0.44**	**4.03**	**0.049**
5	(Water level April –2)	x	(0.03)	(0.42)	(2.61)	(0.112)
6	**Semi-annual temperature –0**		**0.03**	**0.45**	**3.44**	**0.069**
Prewhitened time series						
1	**Temperature October –3**		**0.09**	**0.09**	**6.07**	**0.017**
2	**Water level March –1**		**0.06**	**0.15**	**3.86**	**0.054**

Note: The respective contributions of climatic factors to variance in smelt landings correspond to the partial R^2, and the multiple R^2 corresponds to cumulative R^2 values. The climatic factors significant at $p < 0.10$ in the multiple regression are in bold and the global R^2 of each multiple regression is underlined.

the main route for freshwater outflow is directed along the south shore of the estuary (Laprise and Dodson 1989 and references therein). Thus, high discharge may reduce the efficiency of passive retention, resulting in an increase in downstream transport out of the St. Lawrence middle estuary of larvae and juveniles. This hypothesis may also apply to the major prey items of smelt, thus reducing survival at all life-history stages. Significant correlations between water level and smelt landings that occur without lag suggest that hydrological conditions prevailing during the summer of capture directly influence the survival of adult fish or catchability (see below). Although the assertion is speculative, strong flows in shoal habitat may be considered generally detrimental to all life-history stages of the south-shore smelt population that spends its entire life cycle in shallow waters (F. Lecomte and J.J. Dodson, unpublished data).

In contrast to the south-shore population, both temperature and water level appear to be equally important in influencing the abundance of the north-shore population. Average temperature measured over the entire growing season during the same year as the landings (uncorrected data) or two years prior to landings (prewhitened data series) influenced the abundance of the north-shore population. Higher temperatures will favour growth, which in turn favours survival, particularly for young-of-the-year fish exploiting the estuarine turbidity maximum (Sirois and Dodson 2000). The growth of smelt prior to reproduction is extremely variable and depends on temperature (McKenzie 1964; Fournier and Landry 1990), which in turn influences recruitment and the size or the age at which smelt enter the fishery. Temperature also influences production cycles of prey and trophic structure. The positive effect of high discharge on the abundance of this population may also act through the trophic dynamics and the physical extent of the estuarine turbidity maximum, which is exploited by the north-shore smelt throughout most of their life cycle. However, the biological mechanisms linking observed trends in temperature, discharge, and smelt population abundance in the estuarine turbidity maximum are complex and in the absence of more complete information, we may only speculate about their nature.

The fact that many of the correlations between catches and environmental variables were strongest during the year of the capture may suggest that temperatures and water levels affect the catchability of the smelt. We cannot completely refute this possibility. To a certain extent, catchability and abundance are positively related. Trap nets will be more efficient in catching fish when there are high densities of fish in the vicinity. However, several lines of evidence suggest that catchability is not a significant factor affecting landings. If catchability were a function of climatic variables, we would expect the varying catchability of trap nets to be reflected in the landings of all species of fish caught in the nets. Yet there was no relationship between smelt catches and the abundance of other fish species caught in the same nets. Furthermore, the absence of a relationship between the number of fisherman and smelt landings suggests that fluctuations in abundance dominate the variation in smelt catches. The annual smelt landings used in this study represent the integra-

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tion of catches over a period of eight months and over a distance exceeding 100 km on both shores, thus decreasing the effects of short-term events such as wind, tides, and temperature variations on catchability. If variation in landings were significantly influenced by catchability, then years of low landings measured over hundreds of kilometres and during periods of months would imply major movements of fish outside fishing zones either across or along the estuary. This is not consistent with the important degree of genetic segregation that is observed between adjacent populations of smelt (Bernatchez and Martin 1996; Lecomte et al. 1999).

Regardless of the biological mechanisms responsible for the differential response of the two sympatric smelt populations to water level and temperature, it is evident that they are responding as two independent biological entities and as such should be considered as Evolutionary Significant Units (ESU; Waples 1995) for conservation and management purposes. An ESU is a population or group of populations that is substantially reproductively isolated from other conspecific population units and represents an important component in the evolutionary legacy of the species (Waples 1995). This definition provides criteria for the identification of ESUs, which are based on genetic isolation and the ESU's contribution to the ecological and genetic diversity of the species. This is particularly appropriate in the present case, as the persistence of the sympatric smelt populations will depend greatly on future climate change. The climate changes expected in the Great Lakes – St. Lawrence River basin might result in significant changes in water supply and temperature. Some authors expect a 40% decrease in water discharge in the St. Lawrence River in future years (Mortsch and Quinn 1996). Such extremely low water discharge was previously observed in the 1930s and 1960s, and according to the present data series, corresponded to high catches on the south shore and low catches on the north shore. However, the use of historical smelt abundance cycles described in the present study to predict future abundance cycles must be approached with caution. Apart from the uncertainties inherent in future climate change predictions, factors such as habitat deterioration must be considered in any attempt to predict future trends. Over the past 30 years, many spawning sites and smelt habitats have been disturbed or lost due to extensive fishing activities, agricultural pollution, and severe physical damages in the St. Lawrence River as well as in its affluents involving bank erosion and sedimentation. The Boyer River, located just downstream of de l'Église Brook, was traditionally one of the most important spawning sites on the south shore but was abandoned by spawners in the 1980s (Trencia et al. 1989). The south-shore population is presently the object of an enhancement program, the major objective of which is to restore the Boyer River spawning grounds (Trencia et al. 1989). Lower discharge should be advantageous for the south-shore smelt population and all efforts to enhance the south-shore population may have their greatest chance of success during periods of low discharge. In contrast, the north-shore population cannot be expected to respond in a similar fashion. High discharge and increased temperatures may favour the north-shore population. Finally, the differential response of the two smelt populations also serves to illustrate the fundamental ecological differences existing between shoal and channel habitats, suggesting that future climate changes may differentially effect other populations or species that are segregated between these two habitats. For example, populations of the copepod *Eurytemora affinis* sampled in the St. Lawrence middle estuary and adjacent salt marshes are genetically highly divergent (Lee 1999). Ecological and genetic segregation between channel and shoal habitat may be a common feature of the St. Lawrence estuarine ecosystem.

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Effects of solar ultraviolet radiation on epilithic metabolism, and nutrient and community composition in a clear-water boreal lake

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Abstract: Stratospheric ozone depletion, climate change, and acidification will increase the exposure of aquatic ecosystems to ultraviolet radiation (UVR; 280–400 nm). The objective of this study was to determine the ecological effects of ambient UVR exposure on epilithon (algal communities attached to rocky substrata) relative to an artificially reduced UVR environment. UVR exposure was altered in the littoral zone of a boreal lake by selectively filtering segments of the solar spectrum with large acrylic sheets. This 130-day study took place at the Experimental Lakes Area, northwestern Ontario, in 1998. Epilithon were monitored for changes in productivity, biomass, pigment, and nutrient and taxonomic composition. The absence of UVR increased epilithic photosynthetic rates 37–46% above epilithon exposed to ambient UVR, increased cellular carbon and nitrogen content, and consequently lowered C:P. UVR effects on algal metabolism were dependent on seasonal trends. Epilithic respiration rates and chlorophyll *a* concentrations were not significantly different among treatments. A reduction in UV induced taxonomic shifts in epilithon, with diatoms increasingly favoured under low UV conditions. Species richness and diversity were not affected. Overall, the results of this study, considered together with previous research, suggest that the epilithic community is sensitive to changes in the UVR environment of aquatic ecosystems.

Résumé : La diminution de l'ozone dans la stratosphère, les changements climatiques et l'acidification vont augmenter l'exposition des écosystèmes aquatiques à la radiation ultraviolette (UVR; 280–400 nm). Le but de notre étude est de déterminer les effets écologiques d'une exposition à l'ultraviolet ambiant sur l'épilithon (la communauté d'algues fixée aux substrats rocheux) par comparaison à une exposition à un environnement où l'utraviolet a été artificiellement réduit. L'exposition à l'ultraviolet a été modifiée dans la zone littorale d'un lac boréal par filtrage sélectif de segments du spectre solaire à l'aide de grandes feuilles d'acrylique. L'expérience s'est poursuivie pendant 130 jours dans la Région des lacs expérimentaux dans le nord-ouest de l'Ontario en 1998. Les changements dans la productivité, la biomasse, les pigments, les nutriments et la composition taxonomique de l'épilithon ont pu être suivis. L'absence d'ultraviolet augmente les taux de photosynthèse de l'épilithon de 37–46% par rapport à l'épilithon exposé à l'ultraviolet ambiant; elle accroît le carbone cellulaire et le contenu en azote et fait ainsi diminuer le rapport C:P. Les effets de l'ultraviolet sur le métabolisme des algues varie selon la saison. Les taux de respiration et les concentrations de chlorophylle *a* de l'épilithon ne sont pas significativement différents d'un traitement à l'autre. Une réduction dans l'ultraviolet amène des modifications dans la composition taxonomique de l'épilithon et les diatomées se trouvent particulièrement favorisées sous un régime de radiation ultraviolette réduite. La richesse en espèces et la diversité ne sont pas affectées. Grosso modo, les résultats de notre recherche, combinés à ceux d'études antérieures, indiquent que la communauté épilithique est sensible aux changements des conditions de radiation ultraviolette dans les écosystèmes aquatiques.

[Traduit par la Rédaction]

Introduction

Stratospheric ozone depletion, climatic warming, and acidification are three of the major human stressors in boreal regions (Schindler 1998). These stressors act synergistically to elevate the exposure of aquatic ecosystems to ultraviolet radiation (UVR; 280–400 nm) (Schindler et al. 1996*a*). Algae can act as valuable indicators of anthropogenic activities that alter the UV environment within aquatic ecosystems. UVB inhibits phytoplankton photosynthetic rates (Karentz et al. 1994; Smith et al. 1992) and growth rates (Jokiel and York 1984). Benthic algae have shown lower

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growth rates (Bothwell et al. 1993), reduced biomass accrual (Bothwell et al. 1994; Vinebrooke and Leavitt 1996; McNamara and Hill 2000), and lower ^{14}C assimilation (Nadeau et al. 1999; McNamara and Hill 2000) in response to UVR. UVR-induced changes in species composition have also been reported for periphyton (algae attached to a substrate) (Bothwell et al. 1993; Vinebrooke and Leavitt 1996; Francoeur and Lowe 1998). UVR damages algal DNA and disrupts the electron transport chain and photosystem II reaction centers (Karentz et al. 1994). Algal inorganic nutrient uptake (Dohler 1992; Hessen et al. 1995), protein synthesis (Behrenfeld et al. 1995), and fatty-acid production (Wang and Chai 1994; Hessen et al. 1997) are also reduced by exposure to UVR.

Investigations of the biological effects of UVR in aquatic ecosystems have often been limited to short-term experiments ranging from hours to days (for examples see McNamara and Hill 2000; Hessen et al. 1997; Smith et al. 1992). More recently, investigations have attempted to incorporate the long-term impacts of UVR on aquatic ecosystems. For example, Vinebrooke and Leavitt (1996, 1998, and 1999*a*) have done many 30-day mesocosm experiments investigating the effects of UVR on periphyton in alpine lakes. Bothwell et al. (1993) found that over 2 to 3 weeks, periphytic diatoms had lower growth rates when exposed to UVR than when exposed to photosynthetically active radiation (PAR) only. However, after five weeks of growth, diatom biomass accrual was reduced in the PAR only treatment owing to differential trophic level sensitivities to UVR (Bothwell et al. 1994). Species composition of algal assemblages has been shown to be different in epilithon (algal communities and associated bacteria, fungi, viruses, and zoobenthos, attached to solid and relatively inert surfaces (Turner et al. 1983)) exposed to varying regimes of UVR in the short term (Vinebrooke and Leavitt 1996). However, little is known about how species composition will respond to altered UVR treatments in the long term. Because length of UVR exposure interacts with multi-trophic level responses and species replacement, short-term investigations are inadequate to explain whole-ecosystem responses to UVR.

The effects of ambient UVR on epilithon were examined in the littoral zone of a clear water boreal lake. Epilithon was exposed to three UV regimes controlled by acrylic filters: PAR (400–700 nm) only, PAR + UVA (320–700 nm), and PAR + UVA + UVB (280–700 nm). A long-term (130 days) experimental design was used to determine whether the effects of UVR are mediated with time. The objectives of this study were to determine if reduced ambient UVA (320–400 nm) and UVB (280–320 nm) exposure on epilithon affects epilithic photosynthetic and respiration rates, biomass, community composition, pigment concentrations, and stoichiometry by testing the following five predictions: (1) photosynthetic rates will be lower in epilithon exposed to UVR than in epilithon protected from UVR exposure because epilithon have been shown to reduce photosynthetic rates when under stress (Turner et al. 1995); (2) respiration rates will be higher in epilithon exposed to UVR than in epilithon protected from UVR due to increased metabolic stress (Odum 1985); (3) algal biomass will be lower in epilithon exposed to UVR due to depressed growth rates (Vinebrooke and Leavitt 1996); (4*a*) epilithic algae will show differential responses to UVR leading to taxonomic shifts among treatments (Vinebrooke and Leavitt 1996; Leavitt et al. 1999); (4*b*) as UVR intensity decreases through the summer and autumn, community composition will converge because UVR is no longer a significant factor affecting growth; and (5) UVR will affect carbon–nitrogen–phosphorus ratios (C:N:P) via a combination of reduced nutrient uptake and metabolic losses of carbon from increased respiration rates (Dohler 1992; Hessen et al. 1995).

Materials and methods

Study area

This study was conducted at the Experimental Lakes Area (ELA), in the boreal region in northwestern Ontario (49°40′N, 93°44′W). The ELA has been described elsewhere (Brunskill and Schindler 1971). The experiment was conducted in Lake 224 (L224). Lake 224, which has been physically, chemically, and biologically monitored since 1974, is a headwater lake with a maximum depth of 27 m, a surface area of 25.9 ha (Brunskill and Schindler 1971), low dissolved organic carbon (DOC) concentrations (2.5–3.5 $mg \cdot L^{-1}$), and high UV penetration (1% of incident UVB at ~2 m) (Schindler et al. 1996*b*).

Experimental design

To determine whether blocking UVR would alter epilithic communities, large plastic optical filters (2.4 × 1.2 m) were set up in L224 to shield epilithon. The filters allowed ~95% of visible light to pass through, while absorbing portions of the UVR spectrum. Three types of filters were used to create the following three UVR treatments: (*a*) PAR (400–700 nm) only (OP-3 acrylic sheets, 3.0 mm thick, 50% transmission at 398 nm), (*b*) PAR + UVA (320–700 nm) (DuPont Mylar-D acrylic sheets, 0.1 mm thick, 50% transmission at 318 nm), and (*c*) PAR + UVA + UVB (280–700 nm) (CYPRO OP4 acrylic sheets, 3.0 mm thick, 70–90% transmittance throughout the UVA and UVB spectra).

The filters were deployed at a water depth of 0.5 m, and secured in polyvinyl chloride (PVC) tubing frames approximately 0.2 to 0.3 m above the lake bottom on rock surfaces of low slope (<10%). The three UV treatments were arranged in a completely randomised block design, with three blocks, along the rocky north shore of L224. A southern exposure was chosen to ensure that daytime shoreline shading was not a factor. Blocks were as similar to each other as possible. The experiment commenced in early June 1998 and ran until mid-October for a total of 130 days.

Unglazed ceramic tiles (114.5 cm^2) were placed under the optical filters to provide an artificial substrate for epilithon to colonize. The tiles were placed at least 30 cm inside the edge of the filters to minimize exposure to light that had not passed through the solar filters first. The tiles were washed overnight in a weak acid bath (1% HCl) before the experiment began to ensure they were clean and uncolonized. Epilithic algal metabolism, biovolume, community composition, pigment concentrations, and nutrient composition were measured from samples collected from the tiles. Samples were collected every two weeks from June to August 1998, and every three weeks in September and October 1998, for a total of eight sample periods. Each block was sampled on a separate day in random order within the same week. The blocks are treated as replicates for statistical and graphical purposes because there were no significant differences between blocks ($p > 0.05$). Sampling dates for block averages are depicted as the median date of the three sampling days within each sample period.

PAR, UV irradiance, and underwater attenuation

PAR and UVR were measured daily at a meteorological site approximately 3 km from L224. PAR was measured with a Li190SA

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LI-COR quantum cosine sensor and incident UVR was measured daily with broadband UVA (320–400 nm) and UVB (300–320 nm) BW-20 sensors (Vital Technologies, Bolton, Ont.), both attached to a Li1000 LI-COR data logger. Broadband voltage UVR measures were calibrated to $W \cdot m^{-2}$ by simultaneously logging broadband data with LI-COR sensors and interval data with a LI-COR model LI-1800UM Spectroradiometer. Daily voltage data were converted to $W \cdot m^{-2}$ using a regression equation calculated by fitting simultaneously recorded volt and $W \cdot m^{-2}$ data. Underwater PAR, UVA, and UVB were monitored three times throughout the summer in L224 at the study site with a submersible LI-COR model LI-1800UM spectroradiometer. UVR attenuation was calculated using DOC data collected five times throughout the summer from L224 and Scully and Lean's (1994) attenuation model.

Epilithic metabolism

Rates of epilithic net photosynthesis and respiration were measured in chambers placed under the optical filters, by measuring the changes in dissolved inorganic carbon (DIC) that occurred in the water overlying samples of epilithon. Two colonized tiles were placed for 1.5 to 2.0 h in each of three transparent and three dark chambers (0.69 L) (made with OP4 and 0% transmittance black acrylic, respectively) filled with lake water (Turner et al. 1983) to measure photosynthesis and respiration, respectively. All incubations were carried out simultaneously between 09:00 and 12:00 to expose the epilithic communities to the same solar radiation intensities. Water samples (10 mL) from each chamber were collected with syringes before and after incubation. Concentrations of DIC were determined using an infrared gas analyzer (Turner et al. 1983). The coefficient of variation of the method was approximately 1% at 100 $\mu mol\ C \cdot L^{-1}$. The same tiles were used to measure metabolism (both respiration and photosynthesis) on each sampling date. Changes in DIC were adjusted for the ratio of water volume to area of epilithon enclosed and then expressed as an areal rate ($\mu mol\ C \cdot m^{-2} \cdot h^{-1}$). The rates measured reflect the activities of the entire epilithic association (Turner et al. 1995).

Epilithic algal biovolume, community composition, and nutrient composition

Epilithon were collected for taxonomic, chlorophyll, carbon, nitrogen, phosphorus, and chlorophyll *a* analyses from three tiles from under each solar filter on each sampling date. Each tile was removed from under the filters and sampled only once. Epilithon was scraped from the tiles using toothbrushes. Composite suspensions were created by combining the three epilithon samples collected from under each optical filter (total area of 3 tiles = 343.5 cm^2). Each composite suspension from under each optical filter was considered one replicate. Three replicates were collected for each treatment (one from each block) in every sampling period. Each composite suspension was diluted to 1000 mL and three 10-mL subsamples were taken to analyze carbon/nitrogen, phosphorus, and chlorophyll *a* content (one subsample for each analysis). Each 10-mL subsample was filtered (Turner et al. 1987), frozen, and analyzed according to Stainton et al. (1971) (carbon, nitrogen, and phosphorus analyses) and Vinebrooke and Leavitt (1999*a*) (chlorophyll *a* analyses, see below).

Two 20-mL subsamples from each composite suspension replicate were preserved for taxonomic analysis and biovolume estimation using acid Lugol's solution at a concentration of 4% of final volume. These subsamples were sonicated to break apart detrital clumps. After sonication, 2 mL was taken from each 20-mL replicate of each treatment on each date and combined to create a composite sample. One composite sample per treatment was analyzed on four dates (each month the experiment was run) for taxonomy and biovolume estimates. Algae were classified to species (genus when not possible) and enumerated by $cells \cdot cm^{-2}$ and cellular volume ($\mu m^3 \cdot cm^{-2}$) for each taxon. The Shannon-Weiner index (H′) was calculated as a measure of taxonomic diversity using biovolume estimates.

Chlorophyll *a* analyses

The frozen filters from pigment subsamples were freeze-dried for 72 h and extracted in the dark for 24 h at 4°C using a solution of 80% acetone – 15% methanol – 5% water. The extracted solutions were filtered through 0.2-µm nylon filters and dried under nitrogen gas. The dried extracts were then frozen and stored in the dark. Dried extracts were dissolved in a known volume of injection solvent (70% acetone – 25% ion-pairing reagent – 5% methanol). Dissolved pigments were separated using a Hewlett Packard (HP) model HPLC (Vinebrooke and Leavitt 1999*a*).

Statistical analyses

One-way repeated measures analyses of variance (RM-ANOVA) of epilithic photosynthetic rates, respiration rates, chlorophyll *a* concentrations, and nutrients (carbon, nitrogen, and phosphorus) were used to test for the effects of UVR on epilithon productivity and community structure. There were three treatment levels (PAR, PAR + UVA, and PAR + UVA + UVB) and eight levels of time (eight sample periods). Scheffé's Post Hoc tests were performed to determine which treatments differed from each other in RM-ANOVAs. All data were $\log_{10}$-transformed to account for inequality of variances (Sokal and Rohlf 1969). All statistical analyses were performed using SPSS 9.0 for Windows (SPSS Inc., Chicago, Ill.). In two sample periods, one block was not sampled because of weather conditions. Analyses were therefore conducted with $n = 2$ instead of $n = 3$, for nutrient, stoichiometry, and chlorophyll *a* analyses. Two sets of three subsamples, instead of three sets of three subsamples, were analyzed for photosynthetic and respiration rates, resulting in $n = 6$.

Results

Surface UV irradiation and UV attenuation

Calculated 1% attenuation depths of UVA and UVB, using Sculiy and Lean's (1994) attenuation model based on a mean [DOC] of 3.34 $mg \cdot L^{-1}$, were 2.44 and 1.2 m, respectively (Fig. 1). Based on this attenuation model, the percent transmission of UVB at 0.3 and 0.5 m was 30.9% and 14.2% of surface values, respectively. Measured attenuation using a LI-COR model LI-1800UM spectroradiometer at depths up to 1.0 m are shown for comparison. Measured UVB percent transmission at 0.3 and 0.5 m was 36.2 and 23.7%, respectively.

Incident mean UVA and UVB flux during the metabolic incubations range from 34.5 to 15.3 $W \cdot m^{-2}$ (UVA) and 1.7 to 0.68 $W \cdot m^{-2}$ (UVB) (Fig. 2). UVR was highest in June and July and declined in September and October.

Epilithic metabolism

Net photosynthesis and respiration increased throughout the summer and declined in the fall (Fig. 3). There was a significant effect of time on metabolic rates (RM-ANOVA, $p < 0.001$). Overall, rates of net photosynthesis were 37 to 46% lower in epilithon exposed to UVR (PAR + UVA and PAR + UVA + UVB) than in epilithon in PAR treatment (Fig. 3*a*; RM-ANOVA, $p = 0.025$). UVA was responsible for the decline in photosynthetic rates (Scheffé's tests; PAR > PAR + UVA = PAR + UVA + UVB). There were no significant differences in respiration rates among UVR treatments (Fig. 3*b*; RM-ANOVA, $p = 0.641$).

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Fig. 1. Percent transmission of UVA and UVB in L224 calculated using Scully and Lean's (1994) attenuation model with mean dissolved organic carbon concentration for 1998 (3.34 mg·L^{-1}), and measured with a LI-COR 1800UM spectroradiometer. Open circle, solid line, measured UVB; open square, dotted line, measured UVA; solid square, dotted line, calculated UVA; solid circle, solid line, calculated UVB.

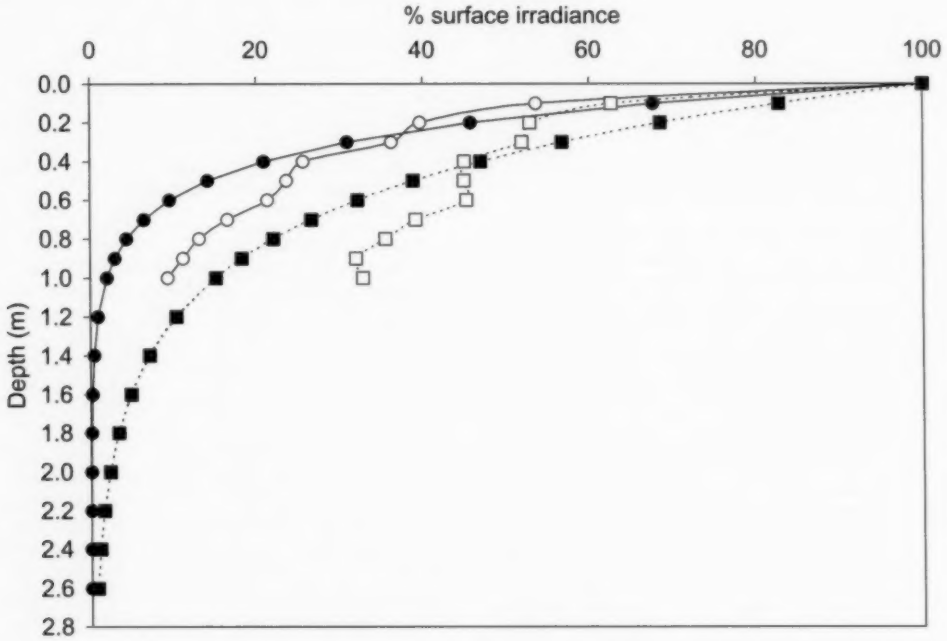
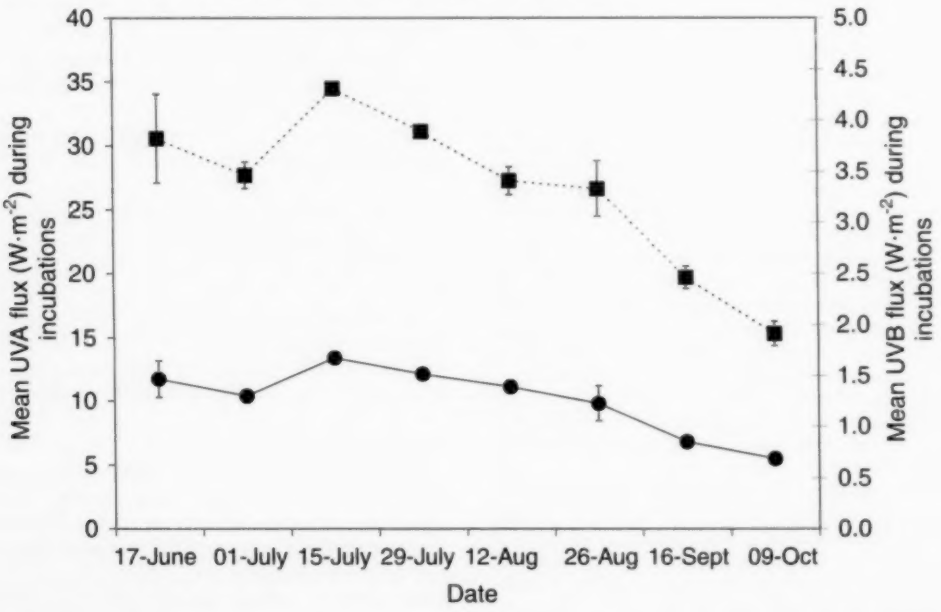


Fig. 2. Mean (±standard error) UVA (primary axis) and UVB (secondary axis) flux during metabolic incubations over eight sample periods (n = 3) in 1998. Solid square, dotted line, UVA; solid circle, solid line, UVB.



The effects of UVR on epilithon varied seasonally (significant time × UVR interaction; RM-ANOVA, $p < 0.001$). Photosynthetic rates were lower in UV-exposed epilithon in July and August (high UVR) and they converged with rates in epilithon exposed to PAR only in September and October when UVR was lower (Fig. 3*a*). The magnitude of difference of net photosynthetic rates between the PAR and UVR treatments increased as a function of the amount of surface

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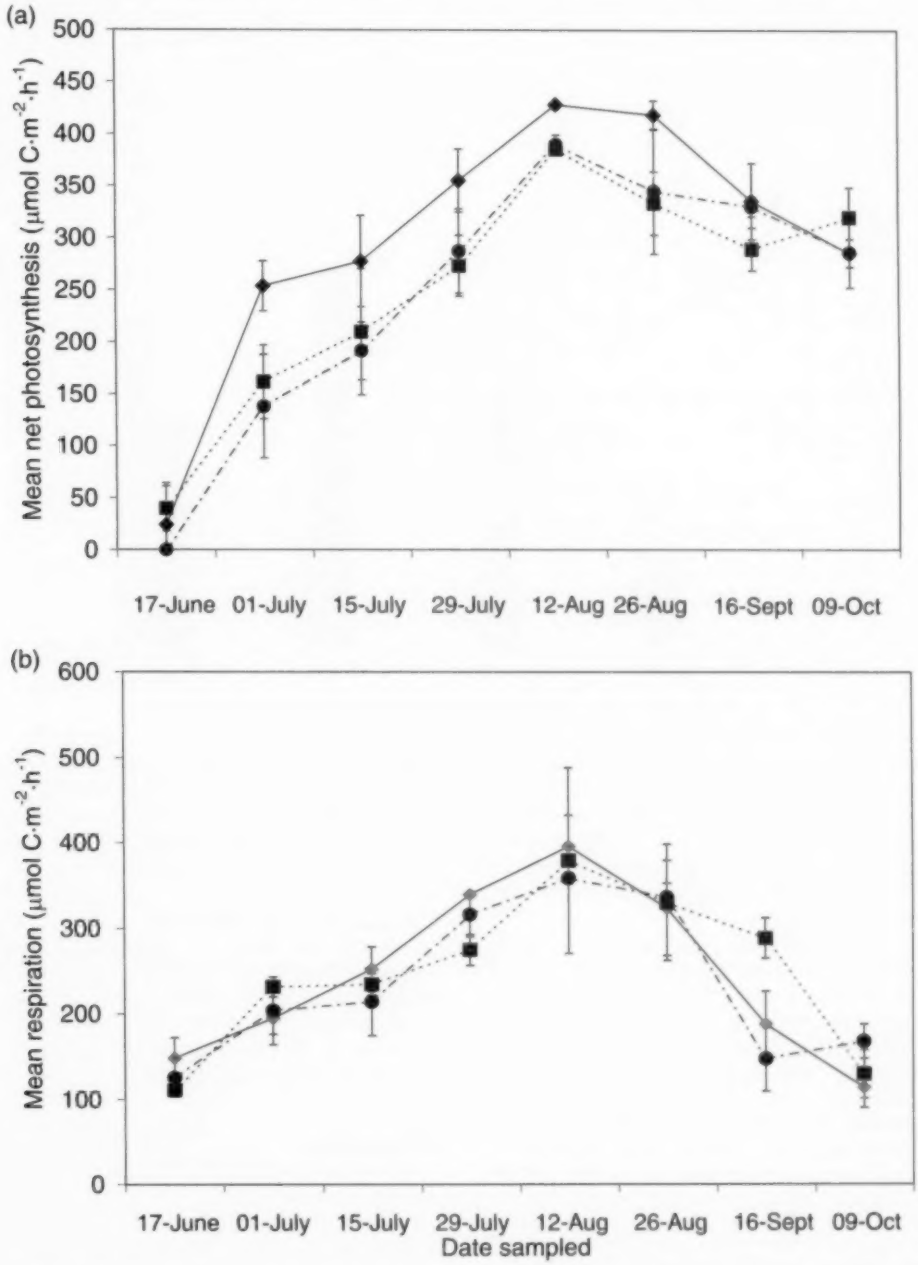
Fig. 3. The mean (n = 3) (±standard error) net photosynthetic rates (µmol C·m^{-2}·h^{-1}) (*a*) and dark respiration rates (µmol C·m^{-2}·h^{-1}) (*b*) for epilithon exposed to three UV treatments in 1998. Diamond, solid line, PAR treatment; square, dotted line, PAR + UVA treatment; circle, broken line, PAR + UVA + UVB treatment.



UVB irradiation during the incubation period. The first sample period in June does not fit these trends, possibly because colonization began only two weeks prior to this sample date.

Epilithic algal biovolume and community composition

Total algal biovolume (µm^3·cm^{-2}) increased in all treatments until August and declined in September (Fig. 4). Epilithon in the PAR treatment exhibited a larger increase in algal biovolume than epilithon exposed to UVR. However, these data must be treated with caution because replicates were not possible (see Materials and methods).

The epilithic communities of all treatments were dominated by diatoms (primarily *Achnanthes minutissima* and *Rhopalodia gibba*) (Fig. 5). Diatom biovolume was higher in the PAR treatment than in epilithon exposed to both levels of UVR in August and September (Fig. 5*a*). Chlorophytes (primarily

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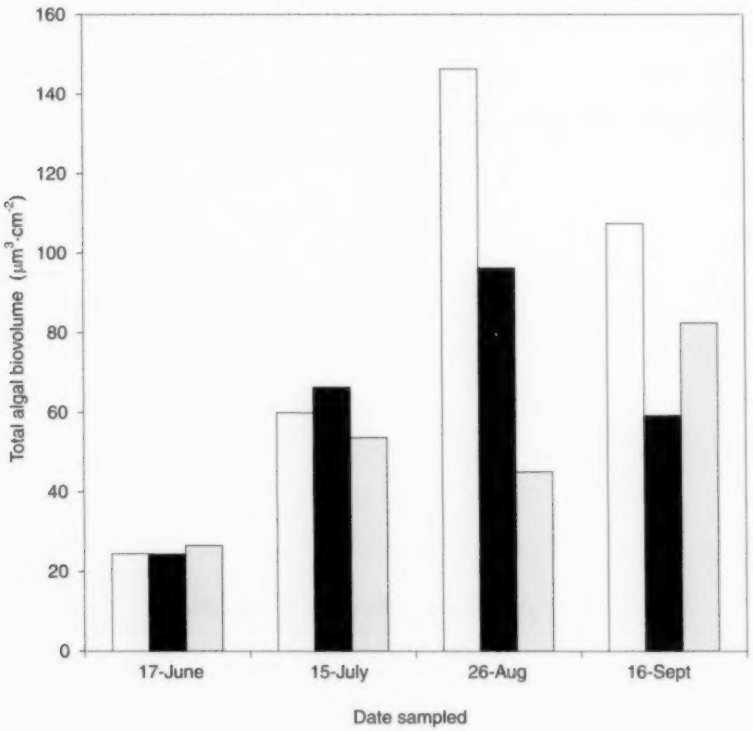
Fig. 4. Total algal biovolume ($\mu m^3 \cdot cm^{-2}$) of epilithon under three UV treatments on four sampling dates in 1998. Each bar represents a composite sample of three replicates. Open bar, PAR treatment; solid bar, PAR + UVA treatment; shaded bar, PAR + UVA + UVB treatment.



Bulbochaete sp.) were second in importance in terms of biovolume in June and July in the PAR treatment, however diatoms and cyanophytes began to dominate in August and September. In the PAR + UVA + UVB treatment, chlorophytes (dominated by *Mougeotia* sp. and *Oedogonium* sp.), and cyanophytes were second in importance throughout all sampling dates (Figs. 5*b*, 5*c*).

Species diversity and richness were similar across all treatments on all sampling dates (Table 1); however, UVR appears to affect community succession. *Mougeotia* sp. was the most abundant chlorophyte in the PAR + UVA + UVB treatment in July and September (approximately 20% of total biovolume from that treatment on those dates). *Achnanthes minutissima* was an important diatom component in all treatments on all dates. *Rhopilodia gibba* dominated diatom biovolume in the PAR treatment, and was primarily responsible for diatoms dominating the epilithic composition, in August and September (Fig. 5*a*).

Nutrient concentrations in epilithon

Epilithic C:P and N:P increased significantly over time in all treatments. In contrast, C:N decreased significantly over time in all treatments (Fig. 6; RM-ANOVA, $p < 0.05$). C:P and N:P were lower in epilithon exposed to UVR (Figs. 6*a*, 6*b*; RM-ANOVA, $p = 0.054$ and 0.033, respectively). C:N was similar in all three treatments (Fig. 6*c*; RM-ANOVA, $p = 0.293$). These results reflect the consistently higher carbon and nitrogen content in PAR treatments than in UV-exposed treatments (Table 2). Although concentrations of cellular carbon, nitrogen, and phosphorus were higher in the PAR treatments (Table 2), RM-ANOVA showed no significant differences among treatments.

Chlorophyll *a* concentrations

Epilithic chlorophyll *a* significantly increased over time in all treatments (Fig. 7; RM-ANOVA, $p < 0.001$). RM-ANOVA showed that the three treatments did not affect chlorophyll *a* concentration (RM-ANOVA, $p = 0.440$). The large variability in the results diminished the sensitivity in detecting UV-dependent changes in chlorophyll *a*.

Discussion

Epilithic metabolism

Ambient UVR suppressed net photosynthetic rates of epilithic periphyton in L224 by 37 to 46% (PAR + UVA and PAR + UVA + UVB treatments) for the first 90 days of this 130-day study. Although few studies have investigated how epilithic carbon metabolism is affected by long-term exposure to ambient UVR, our results corroborate the findings of other studies conducted over shorter durations (2 weeks to 30 days), demonstrating that current levels of UVR have a detrimental effect on algal productivity. Short-term exposure to UVR was found to lower benthic algal ^{14}C uptake rates

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Fig. 5. Biovolume ($\mu m^3 \cdot cm^{-2}$) of diatoms (*a*), chlorophytes (*b*), and cyanophytes (*c*) of epilithon exposed to three UV treatments on four sampling dates in 1998. Each point represents a composite sample of three replicates. Diamond, solid line, PAR treatment; square, dotted line, PAR + UVA treatment; circle, broken line, PAR + UVA + UVB treatment.

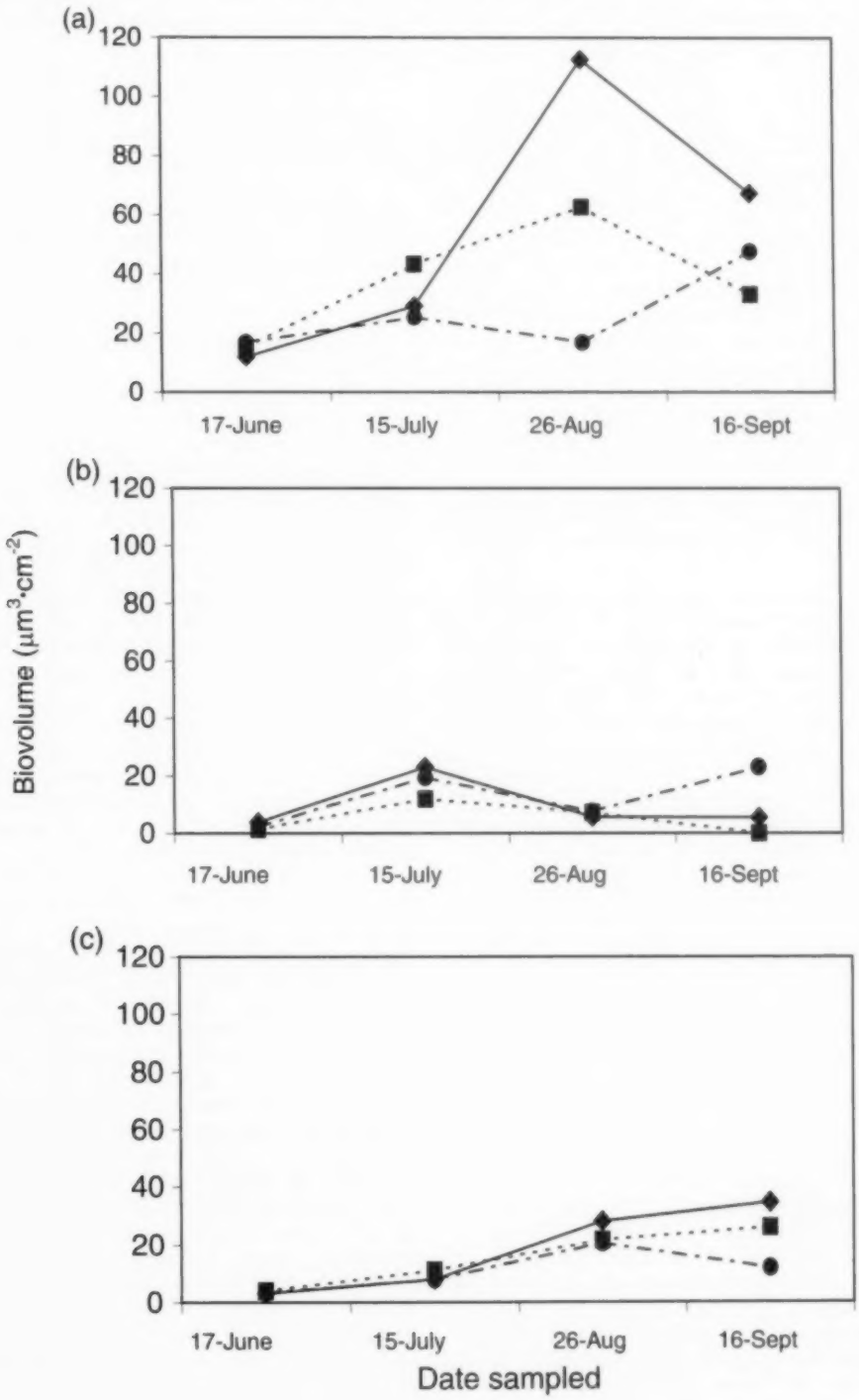

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Table 1. Diversity (H′) and species richness of epilithon in three ultraviolet radiation (UVR) treatments on four sample periods.

	Diversity (H′)			Species richness		
Date	PAR	PAR+UVA	PAR+UVA+UVB	PAR	PAR+UVA	PAR+UVA+UVB
16 June 1998	2.89	2.98	2.92	22	28	23
14 July 1998	2.38	2.70	2.39	19	15	13
25 August 1998	2.72	2.78	2.57	14	16	14
15 September 1998	2.40	2.56	2.86	13	14	17

Note: Numbers represent composite samples from three replicates. PAR, photosynthetically active radiation.

(Nadeau et al. 1999; McNamara and Hill 2000). Similarly, Bothwell et al. (1993) found that short-term daily exposure to UVB led to a 30–40% reduction of periphytic diatom growth rates and restricted diatom biomass accrual in shallow (depth of 1 cm) experimental flumes. Vinebrooke and Leavitt (1996) also discovered a decline of 50% in biomass accrual when periphyton was exposed to ambient levels of UVR for 30 days in a clear water alpine lake. In contrast, Kim and Watanabe (1994) determined that diatoms, which initially exhibited reduced photosynthetic rates in response to UVA exposure, acclimatized after six days to show similar photosynthetic rates to PAR treatments. In our experiment, suppressed photosynthetic rates in response to ambient UVR did not show any signs of acclimation in the first 90 days.

The lower net photosynthetic rates can be primarily attributed to UVA. Other investigators have found that UVA was predominantly responsible for photosynthetic inhibition in phytoplankton (Buhlmann et al. 1987) and inhibited algal growth rates (Kim and Watanabe 1994; Jokiel and York 1984). UVA decreased ^{14}C uptake rates in the light to just above dark uptake rates in Antarctic cyanobacterial mats (Nadeau et al. 1999). However, UV-induced damage to phytoplankton becomes more severe with decreasing wavelengths (Smith et al. 1992) by inactivating photosystems, disrupting electron transport, and destroying pigments and membranes (Karentz et al. 1994). UVB contains more energy per photon than UVA, therefore it is more deleterious per photon; however, UVA is a larger portion of the solar spectrum than UVB, causing the majority of UV photosynthetic inhibition (Karentz et al. 1994).

Epilithic respiration rates in the dark were not different in the PAR and UVR exposed treatments. These results do not support the hypothesis that respiration increases as a functional response to increased stress within the community (Odum 1985). We hypothesized that dark respiration rates would be higher in epilithon exposed to UVR due to increased ATP expenditure to prevent or repair UVR damage. There is little information about the relationship of epilithic respiration to UVR stress. However, in the following year at the same study location, Weidman (2000) found that epilithic dark respiration rates increased significantly in response to UVR after 28 days of growth at a depth of 0.54 m. The epilithic community studied by Weidman (2000) was dominated by chlorophytes, whereas diatoms dominated the epilithon in our study. Further, Donahue (2000) suggested that filamentous chlorophytes may exhibit an increased photorespiratory capacity as a photoprotective mechanism to reduce the UV-induced formation of reactive oxygen species. Our results may not be showing respiration responses to UVR, as previous studies have shown, because the community composition is different than in previous studies.

Epilithic chlorophyll *a*, biovolume, and cellular carbon accrual

There were no significant differences in concentrations of chlorophyll *a* among the three UV treatments in this experiment. Evidence suggests that UVR inhibits algal productivity by the destruction of photosynthetic pigments, such as chlorophyll, or damage to chloroplasts (Xenopoulos et al. 2000). Previous studies have attributed the UV-induced reduction of periphytic chlorophyll *a* concentrations to inhibited periphyton development (Bothwell et al. 1994; Vinebrooke and Leavitt 1996; Francoeur and Lowe 1998). However, it is also possible that chlorophyll *a* declines with increased UVR due to pigment bleaching or photoacclimation (Falkowski and LaRoche 1991). In this study, the lack of change of chlorophyll *a* between treatments, with lower photosynthetic rates in UVR treatments, indicates that damaged or reduced chlorophyll may not be the cause of reduced photosynthesis.

Under the environmental conditions employed in this study, perhaps the levels of UVR were not sufficient to elicit the responses in chlorophyll *a* that were demonstrated in previous studies carried out in environments where UVR was more intense, i.e., higher altitude and shallower depths. For example, Bothwell et al. (1993) found that UVB restricted chlorophyll accrual in shallow (depth of 1 cm) experimental flumes. Francoeur and Lowe (1998) also detected a substantial decline in chlorophyll *a* concentrations in epilithon (6 cm deep) exposed to UVR in a mesotrophic, glacial lake. Vinebrooke and Leavitt (1996) found a decline in chlorophyll *a* when periphyton was exposed to ambient levels of UVR in a clear water (DOC < 1 $mg \cdot L^{-1}$) alpine lake. It is also possible that chlorophyll *a* concentrations were not different among treatments due to high variability in the data.

Biovolume estimates were lower in epilithon exposed to UVR in August and September. These results, combined with consistently lower levels of epilithic carbon content in the UV-exposed treatments, support the hypothesis that algal growth is greater in epilithon blocked from UVR. McNamara and Hill (2000) also found that epilithic biovolume significantly declined in response to artificially increased UVB in shallow (1.5 cm deep) experimental streams. Biovolume was also lower in periphyton exposed to ambient UVR in an alpine lake (Vinebrooke and Leavitt 1996). The lower algal biomass in epilithon exposed to UVR may be responsible for the lower photosynthetic rates.

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Fig. 6. Mean (±standard error) epilithic molar C:P (*a*), N:P (*b*), and C:N (*c*) upon exposure to three UV treatments over eight sample periods (n = 3) in 1998. Diamond, solid line, PAR treatment; square, dotted line, PAR + UVA treatment; circle, broken line, PAR + UVA + UVB treatment.

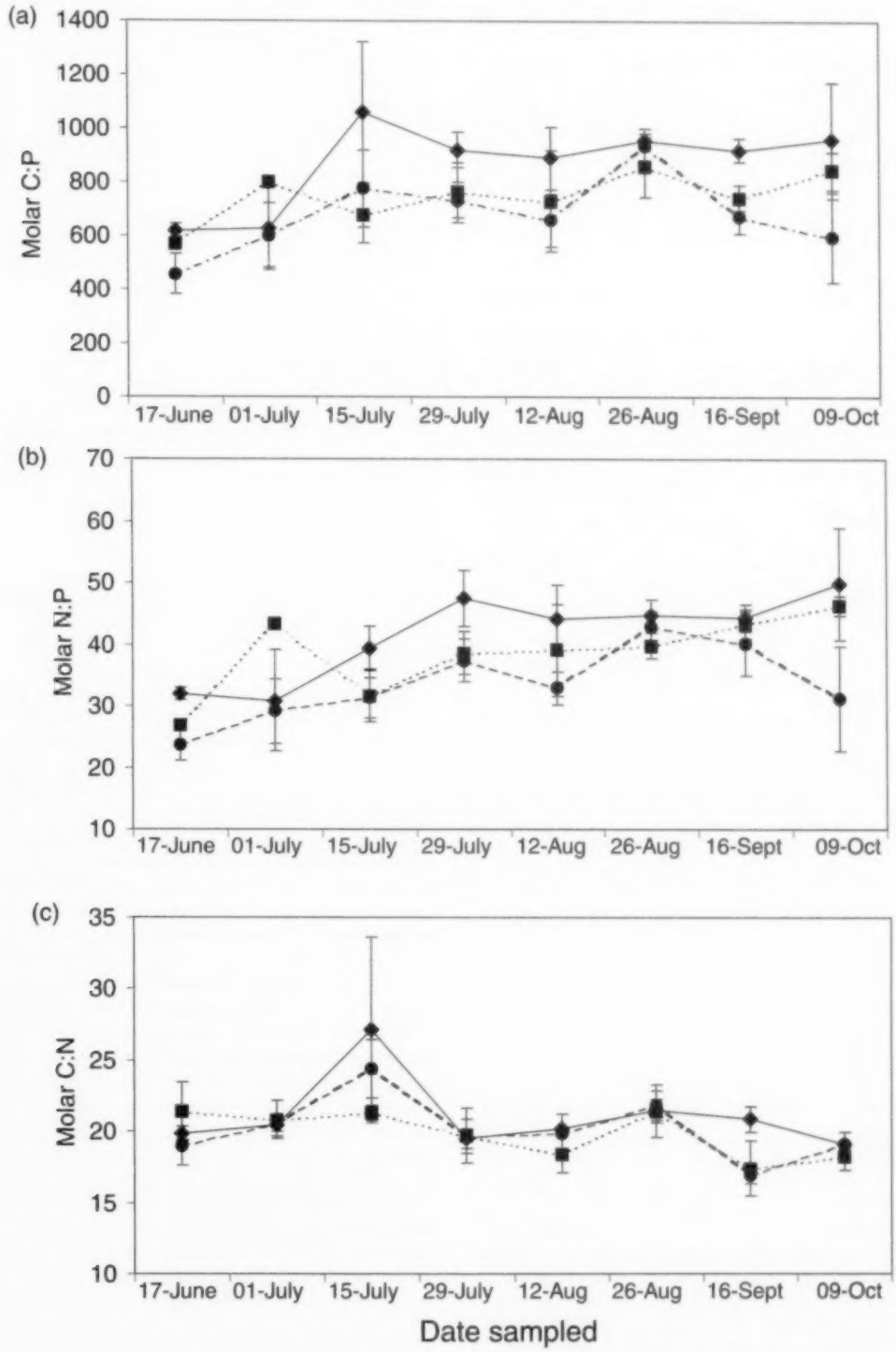

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Fig. 7. Mean (±standard error) chlorophyll *a* concentrations (μg·m^{-2}) for epilithon exposed to three UV treatments over eight sample periods (n = 3) in 1998. Diamond, solid line, PAR treatment; square, dotted line, PAR + UVA treatment; circle, broken line, PAR + UVA + UVB treatment.

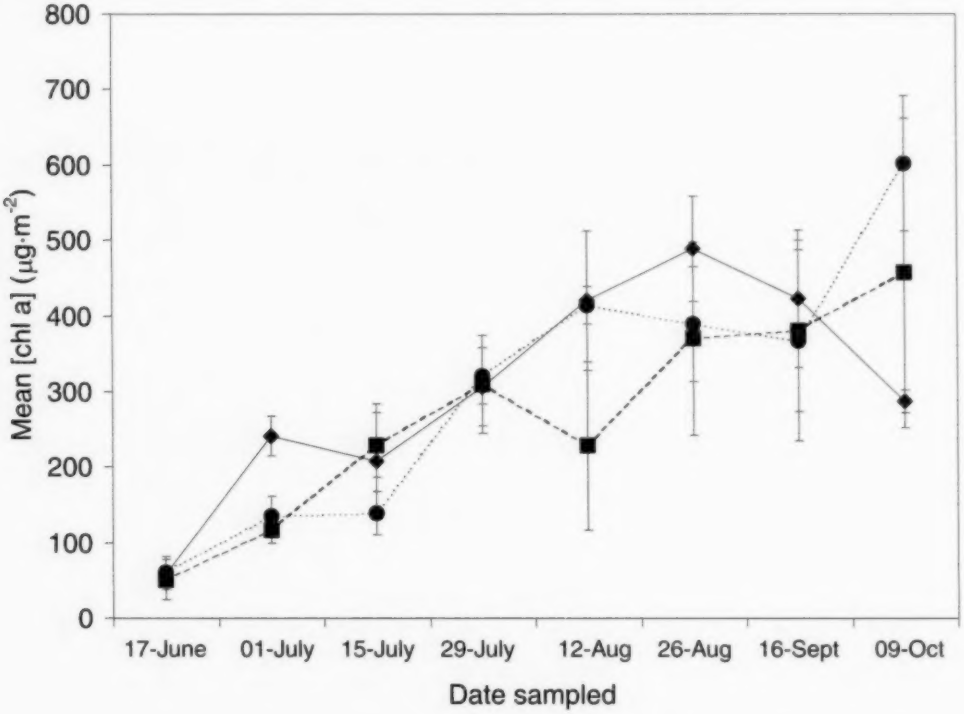

Table 2. Seasonal mean (n = 3) epilithic carbon, nitrogen, and phosphorus (μg·cm^{-2}) (n = 19) collected in seven sample periods (first sample period excluded) in three ultraviolet radiation (UVR) treatments (±standard error).

Treatment	Carbon	Nitrogen	Phosphorus
PAR	283.77 ± 29.77	18.20 ± 1.72	0.83 ± 0.09
PAR+UVA	226.92 ± 31.57	15.38 ± 1.95	0.71 ± 0.10
PAR+UVA+UVB	202.25 ± 19.95	13.97 ± 1.39	0.77 ± 0.07

Note: PAR, photosynthetically active radiation.

UV-related changes in algal community structure

There is evidence for UV sensitivity in diatoms in our study. Diatoms were the dominant algal group in the PAR treatment in August and September, whereas they were less prominent in the UVR-exposed treatments. These data support recent findings that diatoms appear to be indicators of low-UV conditions (Vinebrooke and Leavitt 1996; Francoeur and Lowe 1998). Leavitt et al. (1999) found that as UV increased eightfold following acidification of L302S, pigments corresponding with diatoms declined 50%. Vinebrooke and Leavitt (1999*b*) found that a decrease in diatoms accounted for the decline in benthic algal biomass associated with increasing elevation in a survey of 20 mountain lakes and ponds. As a result of higher incident UVR and lower DOC concentrations, the inhibitory effects of UVR on periphyton may be more damaging in high-elevation and acidified lakes. Similarities in diatom sensitivity among UVR-exclusion experiments and acidified and alpine lakes suggest that the similarities between algal assemblages in alpine and acidified lakes may be at least partly because of interspecific UVR adaptations.

Rhopalodia gibba accounted for the higher diatom biomass in the PAR treatment in this experiment and in the study done by Francoeur and Lowe (1998). This diatom contains cyanobacterial endosymbionts capable of fixing atmospheric nitrogen (Stevenson et al. 1996). UVR may have greater effects on benthic communities in low nitrogen habitats, because the dominant species (nitrogen fixers) are highly UVR sensitive (Francoeur and Lowe 1998). Future studies will be required to determine how UV affects nitrogen assimilation in algal assemblages.

Chlorophytes made up a larger proportion of the algal assemblages in treatments exposed to UVR than in PAR treatments. *Mougeotia* sp. (a filamentous chlorophyte) was responsible for this trend in July and September. Turner et al. (1995) found that green algae (particularly *Mougeotia* sp.) are abundant in acidified lakes. It is possible that under natural conditions, *Mougeotia* sp. is competitively excluded, but once higher-UV conditions occur (i.e., owing to reduced DOC during acidification), the UV-sensitive diatoms are suppressed, allowing the slower-growing *Mougeotia* sp. to dominate. Donahue (2000) also found that filamentous chlorophytes dominated the shallowest, highest UV and PAR exposure sites in a survey at the ELA. In our study,

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Mougeotia sp. was more abundant in epilithon exposed to ambient UVR conditions than epilithon exposed to reduced levels of UVR, which, in combination with previous studies, suggests that *Mougeotia* sp. increases as a function of increasing UVR in the aquatic environment.

Although algal taxonomic composition diverged as a result of different UV regimes, species richness and diversity remained relatively unchanged. In contrast, Vinebrooke and Leavitt (1996) found that species richness was lower in epilithon exposed to ambient UV than in epilithon in reduced UV treatments after 30 days. In September of our experiment, as incident UV declined and hence treatment effects became negligible, the taxonomic composition in the three UV treatments remained different. This indicates the community composition may be determined at the colonization stage.

Food quality

Carbon–phosphorus ratios (C:P) and nitrogen–phosphorus ratios (N:P) were both lower in epilithon exposed to ambient UVR than epilithon exposed to reduced UVR treatments in this study, consequently increasing food quality (Sterner et al. 1993). A higher food quality in epilithon exposed to UVR is counterintuitive because others have found that algal nutrient uptake (Dohler 1992; Hessen et al. 1995), protein synthesis (Behrenfeld et al. 1995), and fatty-acid production (Wang and Chai 1994; Hessen et al. 1997) are inhibited by UVR. Previous studies have found cellular carbon, nitrogen, and phosphorus content were not affected by reductions in ambient UVR and artificially increased UVR (Weidman 2000, and McNamara and Hill 2000, respectively). It is possible that the lower carbon uptake rates of epilithon exposed to UVR in this study may have driven C:P down.

There was more cellular nitrogen in algae from our PAR treatment than in the UVR-exposed treatments, suggesting that nitrogen uptake may have been inhibited in algae exposed to UVR. Similarly, ^{15}N uptake was reduced in diatoms under UVB irradiance (Dohler 1992). Ammonium and nitrate uptakes were also inhibited in algae exposed to UVB (Behrenfeld et al. 1995). The stoichiometric trends in our experiment may reflect the taxonomic differences in the epilithon exposed to varying UV treatments. *Rhopilodia gibba*, which contains N-fixing symbionts, was more abundant in epilithon with higher N:P (PAR treatment). High N:P may be the outcome of an N-fixing dominated algal community in the PAR treatments (Sterner and Hessen 1994).

In summary, epilithon exposed to ambient UVR had lower primary production than in epilithon blocked from UV exposure, and varying UV regimes induced taxonomic shifts in the epilithic algae. Epilithic communities did not converge among treatments once UV declined owing to seasonal trends, lending support to the argument that communities are most susceptible to UVR during early stages of colonization. Epilithic C:N:P is affected by UVR, indicating that future research is necessary to determine the effect of UVR on the elemental composition of epilithic biofilms and the consequences of food quality for benthic grazers. In conclusion, this study, considered together with research conducted in shallower (Bothwell et al. 1993, 1994; McNamara and Hill 2000) and higher altitude (Vinebrooke and Leavitt 1996) habitats, suggests that the epilithic community is responsive to changes in the UVR environment of aquatic ecosystems.

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PERSPECTIVES

Exploitation trajectory of a declining fauna: a century of freshwater mussel fisheries in North America

James L. Anthony and John A. Downing

Abstract: Freshwater mussels (Bivalvia: Unionidae) have been an economically valuable biological resource in North America since the mid-1800s. Although the industries based upon mussel harvest are quite distinct from one another, the trends apparent in harvest statistics are remarkably similar among each successive harvest era. Whether fished for freshwater pearls, button production, or cultured pearl production, market factors have driven commercial harvests while the life history and ecology of mussels have been largely ignored. Annual yields of freshwater mussels are declining throughout the United States and catch per unit effort (CPUE) has declined dramatically in some of the most important American mussel fisheries. Harvest statistics indicate that mussel populations are dangerously depleted due to the erosion of the latest industry based upon their harvest. It seems likely that the exhaustive harvests of both the distant and recent past, coupled with habitat loss and degradation, have left North American unionid mussel populations at levels insufficient to support the substantial harvests consistently demanded by industry. This century-long exploitation trajectory provides valuable lessons about the mechanisms of fisheries collapse that are necessary to ensure the sustainable management of aquatic resources.

Résumé : Les moules d'eau douce (Bivalvia: Unionidae) constituent une ressource biologique d'importance économique considérable en Amérique du nord depuis le milieu du 19e siècle. Bien que les diverses industries basées sur la récolte des moules soient différentes les unes des autres, les tendances dans les statistiques de récolte sont remarquablement semblables au cours des différentes périodes de récolte qui se sont succédées au cours du temps. Que les récoltes aient été faites pour la collecte de perles d'eau douce, la fabrication de boutons, ou la production de perles cultivées, les forces du marché ont contrôlé les récoltes commerciales, alors que le cycle biologique et l'écologie n'ont pas été en grande mesure pris en compte. Les rendements annuels de moules d'eau douce décroissent partout aux États-Unis et les captures par unité d'effort (CPUE) ont décliné de façon spectaculaire dans quelques-uns des plus importants sites américains de récolte de moules. Les statistiques des récoltes indiquent que les populations de moules sont dangereusement hypothéquées au moment où l'industrie la plus récente basée sur les moules est en train de s'effriter. Il semble probable que les récoltes exhaustives du passé lointain et du passé plus récent, combinées à la perte et la dégradation des habitats, ont laissé les population nord-américaines de moules unionidés à des densités qui ne permettent plus les récoltes intensives requises par l'industrie. L'histoire de cette exploitation centenaire fournit des enseignements précieux sur les mécanismes d'effondrement des pêches, renseignements qui sont indispensables pour mettre sur pied une gestion durable des ressources aquatiques.

[Traduit par la Rédaction]

Introduction

North American freshwater mussels (Bivalvia: Unionidae) are valuable components of freshwater biodiversity. Through their suspension feeding, these slow-growing long-lived organisms (Anthony et al. 2001) may influence phytoplankton ecology (Daukas et al. 1981), water quality, and nutrient cycling (Nalepa et al. 1991). Mussels may also constitute a significant proportion of the freshwater macrobenthic biomass (e.g., Negus 1966) and their obligate parasitic larvae can impact fish mortality (Matteson 1948).

Historically, the importance of freshwater mussels has not been solely ecological, however. Although mussels may have provided a valuable supplemental food source to indigenous peoples for centuries prior to European settlement (Parmalee and Bogan 1998), large-scale commercial interest in these freshwater bivalves did not develop until the freshwater pearl rushes of the mid-1800s (Kunz 1893; Claassen 1994). Soon

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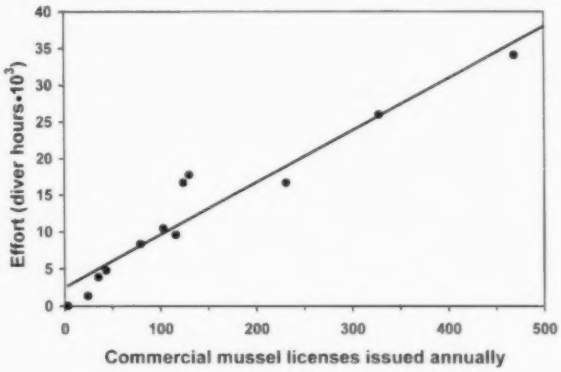
thereafter, many freshwater mussel species were extensively harvested for the production of pearl buttons, and presently, the shells of freshwater mussels, which are ground into spherical nuclei, are the foundation of the multi-million dollar Asian cultured-pearl industry (Thiel and Fritz 1993; Claassen 1994; Fassler 1994).

Despite their ecological and economic importance, the nearly 300 North American unionid mussel species are apparently one of the most rapidly declining components of freshwater biodiversity with nearly 72% of the North American species considered extinct, endangered, threatened, or species of special concern (Williams et al. 1993). The rapid decline of many unionid mussel species has been attributed to commercial exploitation, water quality degradation, impoundment, habitat destruction, exotic species introduction, and watershed alteration (Williams et al. 1993). These substantial declines in unionid mussels will likely have serious implications for both North American freshwater ecology and biodiversity, as well as for mussel fisheries.

Although several attempts to examine United States mussel fisheries have incorporated investigation of short periods of the mussel exploitation trajectory, synoptic examination of a broad time frame is necessary to adequately portray more than a century of extensive harvests. For example, Thiel and Fritz (1993) briefly summarize historic mussel harvests in the Upper Mississippi River, but consider primarily recent harvests and regulations enacted since the 1980s. Similarly, Fassler (1994) provides an extensive synopsis of the market factors that gave rise to and continue to drive the relatively recent cultured-pearl industry. Although Claassen (1994) provides a valuable comprehensive examination of historic and recent mussel industries of the U.S. Mississippi River basin as well as a colorful account of those involved, the focus is primarily upon the social implications of mussel harvest and industry trends rather than the biological ramifications of exhaustive mussel harvest. Several statewide harvest reports also have been published, but most are largely limited to recent mussel harvests or to very localized harvest sites (e.g., Anderson et al. 1993; Hubbs and Jones 1996; Gritters and Aulwes 1998). Some historical overviews of U.S. mussel harvests also discuss harvest yields and their values without normalizing monetary estimates (e.g., Thiel and Fritz 1993; Claassen 1994), making it difficult to evaluate the market factors driving historic mussel fisheries. Most also fail to adhere to the use of the Latin nomenclature of commercially exploited mussel species (e.g., Carlander 1954; Claassen 1994), thereby increasing the difficulty of examining the species-level impacts of mussel harvests.

An understanding of the historical markets and fisheries for freshwater mussels is critical for evaluating the potential effects of future harvests in the U.S. More broadly, however, such an assessment may serve as an important model for other species. This historical perspective goes beyond previously published efforts by providing an overview spanning all phases of exploitation and integrating both catch statistics and economic forces. Furthermore, we include compilations and analyses of long-term time trends in mussel catch statistics that have not been attempted elsewhere. This assessment of historic U.S. mussel fisheries not only provides the holistic view necessary to discern the potential role of harvest on population viability in exploited species, but may also augment our understanding of mussel ecology through a more complete and accurate knowledge of the patterns of commercial harvest that have shaped the present condition of populations.

Fig. 1. Effort (diver hours), 1987–1998, is strongly positively correlated with the number of commercial licenses issued in the state of Iowa's Mississippi River freshwater mussel fishery (r^2 = 0.92). Data are from the Iowa Department of Natural Resources.[2]



Methods

We examined historic and recent commercial harvest statistics compiled by U.S. federal agencies (U.S. Bureau of Fisheries, U.S. Fish and Wildlife Service, U.S. National Marine Fisheries Service) and from various state agencies (e.g., Indiana Department of Natural Resources, Iowa Department of Natural Resources, Kentucky Department of Fish and Wildlife Resources, Missouri Department of Conservation, Wisconsin Department of Natural Resources). Annual estimates of commercial mussel yields, as well as their values, were examined in the context of market trends and regulatory legislation allowing us to attribute probable causation (i.e., market influences vs. mussel population trends) to the many rapid fluctuations evident in annual harvest levels.

Throughout this analysis, it is important to appreciate that mussel catch statistics are generally based only upon those animals actually utilized for button or pearl production and often do not reflect the significant unmarketable by-catch of the actual harvest (Anderson et al. 1993; Claassen 1994). In addition, commercial license holders in many states (e.g., Iowa, Indiana, Tennessee) have only recently been legally obligated to report their yields to state agencies (Anderson et al. 1993; Todd 1993; Gritters and Aulwes 1998). Many estimates of annual harvest are therefore based upon the report of only a limited proportion of the actual mussel harvest and are therefore substantial underestimates of that actually harvested. Where the proportion of reporting license holders is known, however, we have extrapolated harvest levels in an attempt to correct for the unreported proportion of the harvest. All historic nomenclature has been revised to reflect presently accepted unionid taxonomy following Parmalee and Bogan (1998).

Estimates of catch per unit effort (CPUE) are rare in the commercial mussel fishery statistics. Alternatively, commercial licensing numbers are more readily available. We have therefore attempted to use yield-per-license as a surrogate of CPUE where CPUE data

[2] S. Gritters, Iowa Department of Natural Resources, Guttenburg Fisheries Office, 331 S. River Park Dr., Guttenburg, IA 52052, U.S.A., unpublished data.

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do not exist. In the state of Iowa, where both effort (diver hours) and license data from 1987 to 1998 have been recorded (Gritters and Aulwes 1998), we have observed that effort is strongly correlated with the number of commercial licenses issued (r^2 = 0.92) (Fig. 1). It therefore seems probable that yield per license is a valid surrogate of CPUE from the present, back through at least the mid-1980s. It is unknown to what degree the strong correlation between diver effort and license numbers may be extended to other methods of taking mussels including brailing and dredging. For this reason, where yield per license data from other states are used as a surrogate of CPUE, the results are interpreted with caution.

All monetary estimates provided here are normalized to reflect the 1998 value of the U.S. dollar. This allows us to accurately compare monetary values of industries and yields at any point during the nearly 150-year history of extensive commercial mussel harvest. Failure to do so could lead to an erroneous representation of the market factors driving commercial mussel harvest, and to underestimation of the true magnitude of the economic value of early harvests.

Results and discussion

Freshwater pearl era: 1850–1900: development and history of the industry

The freshwater pearls created by unionid mussels were esteemed by North American aboriginal cultures long before the arrival of the first Europeans to this continent (Kunz 1893; Ward 1985). Likewise, the first extensive North American mussel harvests of the 19th century were fueled by an increasing demand for these freshwater counterparts of the already popular marine pearls (Kunz 1893). Despite the existence of few statistics for these early harvests, these pearl rushes are important in both historical and ecological contexts. Although often ignored, profits from early pearl rushes, such as those in New Jersey (1857), Iowa (1860), and Arkansas (1897) (Kunz 1893), surpassed those of several important U.S. industries including mining and petroleum production (Claassen 1994).

Historical mussel harvests for freshwater pearls were governed largely by boom-and-bust trends. Large-scale migrations of pearl prospectors often followed the discovery of pearls. For example, the discovery of a 93-grain (4.65 g) freshwater pearl from Notch Brook near Patterson, N.J., and its subsequent sale for over $60 000 (1998 $U.S.), fueled the exhaustion of mussel beds in Notch Brook and other nearby streams (Kunz 1893). In the years that followed, valuable freshwater pearls from throughout the U.S. were sold in domestic and international markets (Kunz 1893; Shira 1913; Wilson and Danglade 1914).

By 1860, pearlers were extensively harvesting freshwater mussels for pearls in Arkansas, Florida, Iowa, Kentucky, Nebraska, New Jersey, Ohio, Tennessee, Texas, Vermont, Washington, and Wisconsin (Kunz 1893; Claassen 1994). Just as in Notch Brook, all sizes and species of mussels in a stream were quickly harvested until both the supply of pearls and the populations of mussels were exhausted. These unsustainable harvests usually resulted in the search for previously "idle" streams in which the same exhaustive practices were repeated (Kunz 1893; Coker 1914). Although virtually all mussel species were exploited, some were especially renowned for their pearls (Table 1); consequently, they bore the brunt of these early harvests (Kunz 1893).

Table 1. During the mid- to late 1800s, 13 freshwater mussel species, listed here with their pre-1900 Latin nomenclature (Kunz 1893), were renowned for their pearls and became some of the most actively sought species of the 19th century pearl rushes. All Latin nomenclature was revised to reflect presently accepted unionid taxonomy following Parmalee and Bogan (1998).

Present nomenclature	Historic nomenclature
Amblema plicata	*Unio costatus*
Elliptio complanata	*Unio complanatus*
Fusconaia flava	*Unio globus*
Lampsilis abrupta	*Unio orbiculatus*
Lampsilis ovata	*Unio ovata*
Leptodea fragilis	*Unio fragilis*; *Unio gracilis*
Megalonaias nervosa	*Unio undulatus*
Obovaria retusa	*Unio torsus*
Quadrula metanevra	*Unio nodosus*
Quadrula pustulosa	*Unio mortoni*
Unknown	*Unio buddianus*
Unknown	*Unio ellioti*
Unknown	*Unio virginianus*

Even disregarding their exhaustive nature, harvests for freshwater pearls were hardly efficient. Often, not a single pearl in thousands of mussels was discovered. Shira (1913) reported that, of 793 392 individual mussels harvested in Texas, only 53 actually contained pearls. Even worse, relatively few pearls were of marketable quality (Kunz 1893). Owing in part to their limited numbers, however, the value of freshwater pearls surpassed that of marine pearls by 1889 and the already exhaustive harvests intensified (Kunz 1893).

Despite the widespread sentiment that mussel stocks were inexhaustible, the industry was declining and few pearlers remained in states that had previously led the nation in freshwater pearl harvests (e.g., Vermont, New Jersey, Ohio) (Kunz 1893). Marketable pearls had become relatively rare by the onset of the 20th century, although pearling was still important in some locations. As late as 1889, extensive pearling was noted on Wisconsin's Pecatonia and Apple rivers. Harvests of freshwater pearls on Illinois' Mackinaw River remained high as late as 1890 as did those on Iowa's Wolf Creek. Some remaining harvests exclusively for freshwater pearls were also noted as late as 1913 in Louisiana and Texas (Shira 1913) while others continued through 1914 in South Dakota (Coker and Southall 1915), Missouri and Arkansas (Utterback 1914), and Minnesota (Wilson and Danglade 1914).

Some of these remaining harvests were substantial. Pearls gathered in Caddo Lake and its tributaries in Louisiana and Texas were valued at over $1 600 000 (1998 $U.S.) in 1912, during what was even considered a relatively poor season (Shira 1913). By 1919, although mussels were harvested primarily for the production of buttons, freshwater pearls obtained as byproducts of the mussel catch were valued at $3 468 783 (1998 $U.S.), nearly half the value of the shells themselves (Smith 1919). As late as 1921, revenue from the sale of pearls composed up to one third of the average musseler's annual income (Roberts 1921). Substantial pearl harvests such as these became relatively rare, however, and harvests solely for freshwater pearls slowly vanished.

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Conservation during the freshwater pearl era

Not long after the onset of the first extensive mussel harvests, some fishery biologists and malacologists were growing concerned. George Kunz (1893), in a presentation to the American Fisheries Society, called the inefficient, exhaustive harvests of North American mussels "the wholesale destruction" of the resource. Kunz, commenting on less intrusive and nonlethal European methods of freshwater pearl extraction, considered the exhaustive harvests of North American mussels unnecessary and irresponsible and he became one of the first to suggest that protective legislation should be enacted to preserve the mussel resource. J.W. Collins (1893), in a letter to the American Fisheries Society, echoed Kunz's concerns, adding that "no state can afford to neglect legislation on a subject more important". These regards were widely ignored, however, and nearly complete exhaustion characterized the remaining freshwater pearl harvests (Fassler 1994).

The pearl button industry: 1890–1960: development and history of the industry

Prior to the mid 1850s, Americans were reliant upon imports to satisfy their demand for mother of pearl buttons. By 1855, however, American manufacturers had begun to produce buttons from the shells of marine mollusks (Josephsson 1909), although there is published evidence of failed attempts to commercially produce buttons from the shells of freshwater mussels in 1802 in Kentucky (Coker 1919) and in the late 1880s in Tennessee and Illinois (Coker 1919; footnote 3). It was not until the arrival of Johann Frederic Böpple, a German immigrant and button manufacturer, however, that North American freshwater mussels would prove commercially viable in the button trade.

Johann Böpple brought the button industry to the banks of the Mississippi River in Muscatine, Iowa in the late 1880s. In 1886, prior to his arrival in the U.S., Böpple had examined shells from Illinois, principally *Amblema plicata* (formerly *Quadrula undulata*) and *Actinonaias ligamentina* (formerly *Lampsilis ligamentinus*), and concluded that the high-quality North American freshwater mussel shells were suitable for button production. He promptly sold his Ottensen, Germany, button manufacturing business (which generally utilized marine shells, ivory, bone, and buffalo horn) and headed for the U.S. Upon his arrival, Böpple first studied mussel shells from the Sangamon and Rock Rivers of Illinois but was dissatisfied with their quality. With subsequent experimentation on shells of *Lampsilis teres* (formerly *Lampsilis anodontoides*; *Lampsilis fallaciosus*) from the Mississippi River, near Muscatine, Iowa, and *Tritogonia verrucosa* (formerly *Tritogonia tuberculata*) from the Iowa River near Columbus Junction, Iowa, however, Böpple perfected the technology and procedures for producing buttons from freshwater shells.[3]

Imported buttons and marine shell material were inexpensive and available in large quantities, stifling Böpple's attempts to market his product. The McKinley Tariff of 1890, however, substantially increased the prices of these imported goods and created the opportunity necessary to establish freshwater mussel shells as the staple material source of the American button industry (Smith 1899; footnote 3). By 1892, Böpple had begun large-scale production of his freshwater pearl buttons. These buttons (Fig. 2) could be made inexpensively and in large quantities, effectively out-competing the higher priced imports (footnote 3; see also Coker 1919).

Capitalization of the button industry on the shores of the Mississippi River was rapid. By 1899, the seven-year-old industry was valued at over $23 000 000 (1998 $U.S.) (Anonymous 1902) and, 10 years later, the value of the unprocessed shell alone exceeded $7 000 000 (1998 $U.S.) (Coker 1919). Sixty button factories were located in the Mississippi River Valley by 1899, and one year later, 10 more had begun production (Anonymous 1902). Less than 10 years after its inception, the industry supported thousands of workers and played a crucial role in the economies of many river towns (Anonymous 1902). Despite some early failures of inexperienced manufacturers, the pearl button industry continued to grow.[3] Buttons produced using freshwater shells composed nearly 50% of the American button product by 1900 (Josephsson 1909), and by 1905, over two thirds of the mother of pearl buttons produced in the U.S. were made from freshwater mussels (Anonymous 1909). In the latter year, over 100 button factories specializing in freshwater mussel shells were operating in the U.S. (Anonymous 1909). In 1916, the industry's peak production year, the U.S. produced over 5.75 billion buttons valued at over $175 000 000 (1998 $U.S.) (Claassen 1994). The industry remained productive until around 1925 when it began to decline in both output and value (Fig. 3) as labor issues in years prior to the Great Depression and competition with new foreign markets began to take their toll (Claassen 1994).

Japanese button manufacturers entered the American button market by 1907 (Anonymous 1909) and intense competition with these foreign producers quickly led to declines in both production and profit for the American industry (Fig. 3). With cheap available labor, the Japanese producers remained competitive (Anonymous 1909; Roberts 1921) and American manufacturers focused increasingly on the production of only high-grade buttons. The near abandonment of low-grade button production would have forced American manufacturers to cut fewer blanks per shell to avoid the cracked or damaged blanks useful only for low-grade buttons (Claassen 1994). Furthermore, as large mussels grew scarce, fewer high-quality blanks could be produced from remaining smaller individuals. Even though output of buttons per se was declining, this implies that larger harvests were necessary simply to maintain a viable industry. For example, Coker (1914) noted that 900 kg of 10-cm *Fusconaia ebena* shells required around 3200 mussels. Alternatively, 900 kg of 5-cm shells required over 20 000 individuals. Therefore, as beds became depleted of larger mussels in the early 20th century, substantially more individual mussels were necessary to sustain the same level of button production and the rate of depletion was accelerated (Coker 1914). Although competition and overexploitation had apparently taken a heavy toll on the industry, many continue to attribute the rising prevalence of inexpen-

[3] J.F. Böpple, Fairport Biological Station (presently Fairport Fish Hatchery), Iowa Department of Natural Resources and United States Fish and Wildlife Service, United States Bureau of Fisheries, Fairport, Iowa, U.S.A., unpublished data.

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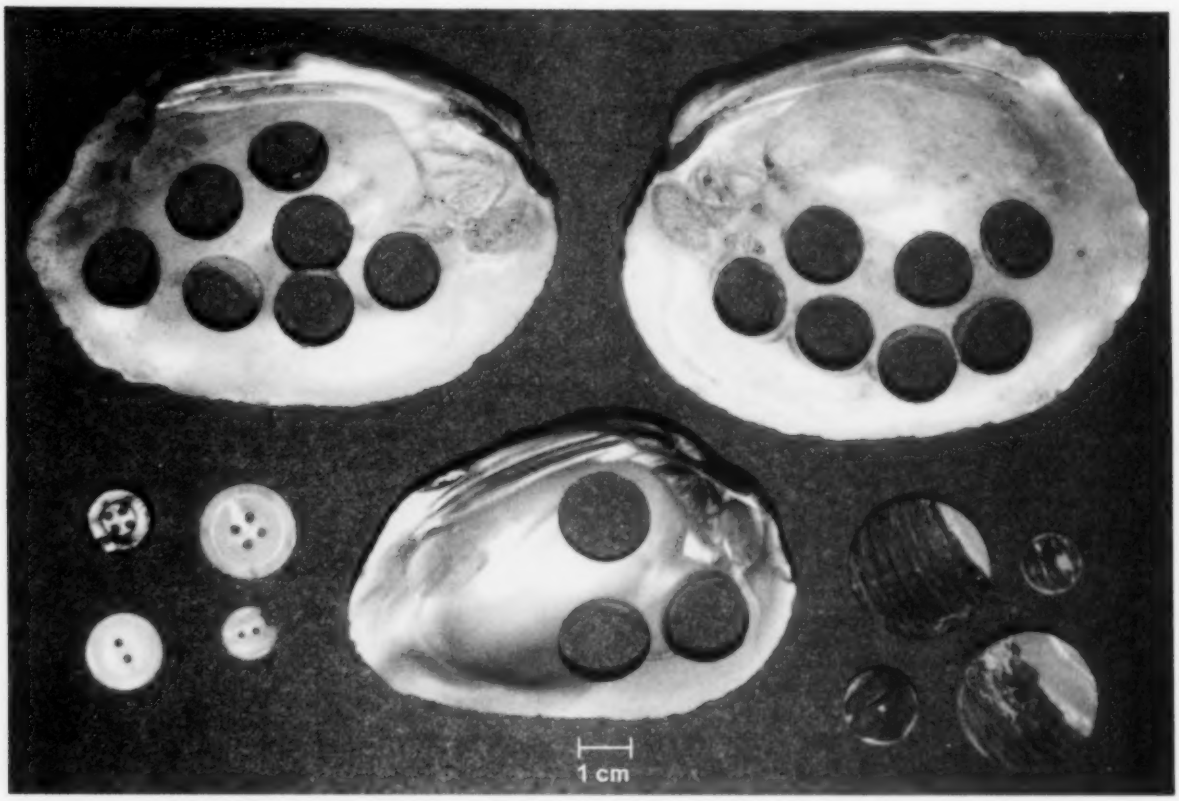
Fig. 2. Round blanks cut from the shells of freshwater mussels were polished into buttons between 1891 and the mid-1960s. Photo by J.L. Anthony.



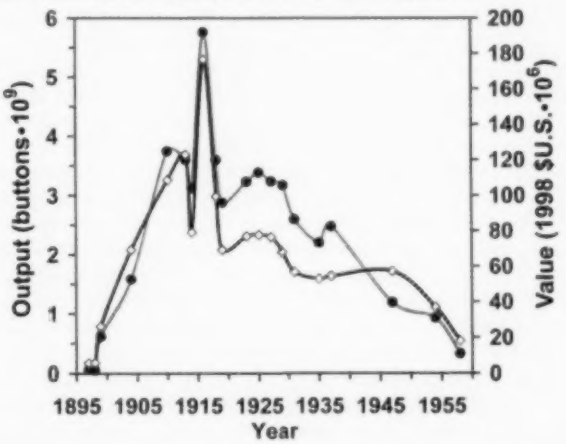
sive plastic buttons through the 1940s to the degradation and eventual demise of the pearl button industry by the mid-1960s (e.g., Claassen 1994; Fassler 1994; Neves 1999).

Mussel harvests and conservation during the pearl button era

The rapid capitalization of the button industry prompted an equally rapid expansion of the freshwater mussel fishery, which began near the first button factories at Muscatine, Iowa (Coker 1914). In 1897, soon after the onset of button production, 3180 tonnes (t) of shells were harvested from the Mississippi River in the immediate vicinity of Muscatine. The following year, 3306 t were harvested, and by 1899 harvests in the same area yielded 21 628 t of mussel shells (Anonymous 1902). These fisheries were lucrative ventures for the thousands they employed and musseler's camps lined the shores of many U.S. streams and rivers (Fig. 4). By 1922, the freshwater mussel fishery was considered one of the largest and most profitable inland fisheries in the U.S. (Rich 1927).

Harvests of freshwater mussels increased to keep pace with the demands of the rapidly growing button industry. In the Peoria Lake stretch of the Illinois River, Ill., two fishermen could expect to harvest over 1.6 t of mussels per day in 1912. In the same river, 27 t and 45 t of shells had been taken at Havana and Bath, Ill., respectively, in preceding

Fig. 3. The U.S. pearl button industry's output in billions of buttons per year (●) and value of the button output as millions of 1998 $U.S. (◇) from 1897 through 1958. The gray (output) and black (value) lines are smooth fits of the market trends of output and value, respectively. Data follow Claassen (1994).



years (Danglade 1912). In 1910, musselers at Keokuk, Iowa removed nearly 1500 t of shells from a 6–8 km stretch of the Mississippi River (Coker 1919), and Roberts (1921) noted

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Fig. 4. Mussel camps and cookout stations lined many U.S. streams in the early 1900s. Note the piles of shell and numerous culled shells lining the banks of the river. A floating cutting station in a white houseboat is visible in the background. Photo from an unspecified location, probably the Illinois River, Ill., in the early 1900s. Photo courtesy of the Peoria Historical Society Collection, Bradley University Library, Peoria, Ill.

that mechanical dredges were capable of harvesting over 9 t of shells daily. Other historical anecdotes suggest that, despite their exhaustive nature, these impressive rates of harvest were not uncommon (Fig. 5).

Musselers often concentrated their exhaustive efforts on small, dense beds of mussels. For example, in 1896, Mississippi River musselers harvested over 450 t of mussels from a bed with an area of just over 1 km^2. This represents harvests of 0.45 $kg \cdot m^{-2}$. Similarly, over 9000 t (12 $kg \cdot m^{-2}$) of shells were taken between 1894 and 1897 from a single bed with an area of less than 0.75 km^2 near New Boston, Ill. (Smith 1898). Smith (1898) estimated that the New Boston catch was composed of over 100 million animals. The exhaustion of relatively small, compact beds was noted after 1900 as well. In 1914, a single harvester removed over 2.7 t of mussels from a bed only tens of meters in length at the outlet of Lake Bemidji, Minn. (Wilson and Danglade 1914). Coker and Southall (1915) noted that a four-person crew had harvested 2.7 t of shell in only three hours from the James River near Milltown, S. Dak.

It was not long before mussel populations throughout the Mississippi River Basin were showing classical signs of overexploitation. Near the onset of exploitation, only the largest and highest quality specimens of the commercial species were marketable (Coker 1914) and many undersized or noncommercial species were likely killed as by-catch (Wilson and Danglade 1914; Coker 1919). Excessive incidental catch of noncommercial or unmarketable individuals may intensify overexploitation, however (Dasgupta 1982). Gradually, economic forces rendered smaller individuals more marketable, prompting the harvest of progressively smaller mussels until beds were nearly exhausted. Even juvenile mussels (<1.25 cm) were often taken to increase the appraised harvest weight, but were simply discarded at the production line (Coker 1914), and it became common for shells <5 cm in length to compose up to 60% of the total catch (Coker 1914, 1919). This classical impact of intense harvest pressure on exploited populations, known as growth overfishing, may result in declining harvest weight and declining average sizes near to or below age at first reproduction (Gulland 1983). It is therefore of no surprise that natural recovery of these exploited beds was rare (Coker 1919). In fact, mussel populations in Iowa's inland streams, which were subject to intense harvest pressure, have never recovered from these exhaustive harvests and are presently nearly extinct (K.E. Arbuckle and J.A. Downing, Iowa State University, Ames, Iowa, U.S.A., unpublished data).

As early as 1899, only seven years after commercial harvests began, many of the formerly dense mussel beds near the button factories at Muscatine, Iowa were depleted (Anonymous 1902). As the quantity of high-quality mussels declined, harvesters actively sought out new beds in streams in surrounding states. This stream-to-stream depletion bears striking similarities to the exhaustive harvests of the pearl rushes

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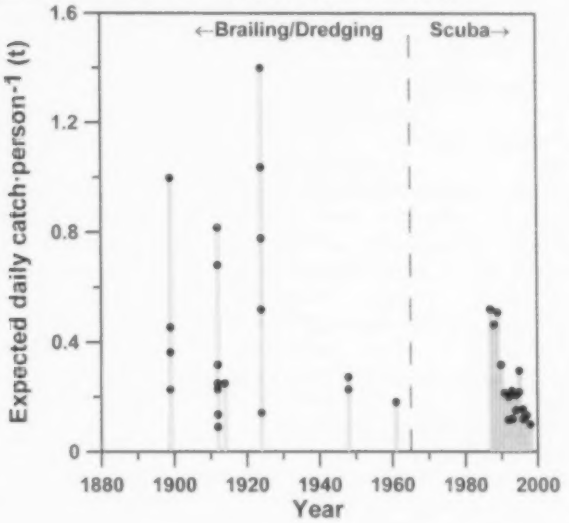
Fig. 5. Anecdotal estimates of daily mussel catch·person^{-1} illustrate a variable but generally declining trend through time. Estimates are from 1899 on the Mississippi River near Muscatine, Iowa (Smith 1899); ~1900 on the Black River near Madison, Ark. (Coker 1914); 1910 on the Black River near Black Rock, Ark. (Coker 1914); 1912 from the Illinois River near Meredosia, Kampsville, Grafton, and Peoria, Ill. (Danglade 1912); 1913 on the Black River near Madison, Ark. (Coker 1914); 1913 on Cross Lake near Pine City, Minn. (Wilson and Danglade 1914); 1914 on Rice Lake, Minn. (Wilson and Danglade 1914); 1924 on Lake Pepin in Minnesota and Wisconsin; 1948 on the Grand River, Mich. (van der Schalie 1948); and 1962 on the Tennessee River, Tenn. (Claassen 1994). Data from 1987–1998 were derived from estimates of CPUE (Hubbs and Jones 1996; Gritters and Aulwes 1998) assuming a 10-h workday. While brailing and dredging were the most common harvest method during early harvests, more efficient methods of harvest (e.g., SCUBA) became dominant after the mid-1960s (Claassen 1994).



and continued until most of the Mississippi River Drainage Basin and many streams of the Great Lakes Drainage Basin were subject to intense commercial harvest pressure (Coker 1914, 1919; Smith 1919).

An escalation of mussel shell prices, due in part to the relative scarcity of high-quality material following the exhaustive harvests of the late 1890s and early 1900s (Claassen 1994), continued even as the overall value of the button industry steeply declined after 1925 (Fig. 3). Further indicative of overexploitation, this allowed musselers to return to beds previously considered depleted and made possible the harvest of others once thought to be uneconomical (Claassen 1994; Neves 1999). The declines in some commercial species led the button industry to accept species that had previously been considered of insufficient quality for button production (Claassen 1994). At least 50 mussel species, 20 of which are presently considered endangered, threatened, or species of special concern (Williams et al. 1993), came to be exploited commercially by the end of the pearl button era (Table 2). It was this shift in the diversity of exploited species that probably allowed the mussel fishery to prolong its support of the industry's demand for shells.

Despite efforts to locate new mussel stocks (e.g., Utterback 1914; Wilson and Danglade 1914; Coker and Southall 1915) and to supplement catch with previously unmarketable species, the degradation of mussel fisheries continued. In 1898, Smith noted that the formerly productive mussel beds near New Boston, Ill. (see above) had been depleted and nearly abandoned (Smith 1898). Rapid and dramatic declines in mussel yields were evident even in the most productive mussel streams. Most of the Illinois River, the most productive mussel fishery in the U.S. between 1907 and 1911, was essentially abandoned by 1912 (Coker 1914). The Wabash River was depleted and nearly abandoned by 1914 (Coker 1914). Similarly, in 1920 musselers largely abandoned mussel beds in Lake Pepin, Minn., which had yielded over 90 t of shells between 1914 and 1919 (Grier 1922). In Arkansas' Black River, individual musselers could expect to harvest over 550 kg·day^{-1} in the late 1800s. By 1914, yields of 45–90 kg·day^{-1} were more typical (Coker 1914). These dramatic declines and the apparent depletion of mussel stocks are not surprising given the low rates of recruitment and slow growth of mussels (Anthony et al. 2001) relative to the high rates of exploitation. Natural stock replacement under these intense harvests was probably negligible relative to fishing mortality.

Extinctions of some mussel species were, by 1908, considered probable in the absence of conservation efforts. Josephsson (1909) stated that "... unless something is done to protect the mussels it will not be long before the raw material for this industry will be exhausted." Biologists and fisheries managers, however, knew little about mussel life histories and growth rates (Lefevre and Curtis 1908). The Fairport Biological Station of the U.S. Bureau of Fisheries was established in Fairport, Iowa in 1909 to answer concerns about depleted mussel stocks and to fill the void in the knowledge of mussel biology (Smith 1919). This was essentially the beginning of mussel conservation in the U.S., but began years after precipitous declines in mussels had been observed (Carlander 1954).

After the establishment of the Fairport Biological Station, and in the face of continued mussel declines, calls for fishery regulations including size restrictions, limited harvest seasons, harvest closures, and rotational harvests became more frequent (e.g., Coker 1914, 1919; Smith 1919). Hugh Smith (1919), then the Commissioner of the U.S. Bureau of Fisheries, stated, "Delay in protecting such a valuable resource is unnecessary and, in the end, fatal." Some were more optimistic, however. Despite widespread stock depletion, Roberts (1921) commented, "There is no reason to fear that our manufacturers of buttons from fresh-water shells will ever lack a supply of the basic raw material."

In response to notable declines in mussel stocks throughout the U.S., Minnesota and Illinois adopted what were apparently the first protective regulations in 1914. The states of Wisconsin and Iowa adopted similar legislation including restrictions on size, means of capture, and licensing fees by 1919 (Smith 1919), while the state of Kentucky enacted its first size restrictions in 1926 (Crowell and Kinman 1993). Unfortunately, these restrictions came only after widespread stock depletion had been noted and were created without accurate knowledge of mussel life history and ecology. Techniques then used to estimate mussel age and growth rates also had no empirical basis and have recently been shown to

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Table 2. At least 50 freshwater mussel species were heavily exploited during the first half of the 20th century for the production of mother of pearl buttons. Historical citations of each species' harvest, and their corresponding nomenclature, are included to unify taxonomic references from some of the most valuable documentation of historical mussel harvests.

Present nomenclature	Historical nomenclature	Source
Actinonaias ligamentina	*Lampsilis ligamentina*	Danglade 1912; Wilson and Danglade 1914; Utterback 1914; Coker 1919; Grier 1926
	Actinonaias carinata	Grier 1926
Alasmidonta marginata	*Alasmidonta marginata*	Grier 1926
Amblema plicata	*Quadrula plicata*	Danglade 1912; Wilson and Danglade 1914; Utterback 1914; Coker 1915; Coker 1919; Grier 1926
	Quadrula perplicata	Coker 1919
	Quadrula undulata	Danglade 1912; Coker and Southall 1915; Coker 1919, Grier 1926
	Amblema costata	Grier 1926
	Amblema peruviana	Grier 1926
Arcidens confragosus	*Arcidens confragosus*	Shira 1913; Coker and Southall 1915; Coker 1919; Grier 1926
Cyclonaias tuberculata	*Quadrula tuberculata*	Coker 1919; Grier 1926
	Quadrula granifera	Coker 1919
	Rotundaria granifera	Grier 1926
Cyprogenia stegaria	*Cyprogenia irrorata*	Coker 1919
Dromus dromus	*Dromus dromus*	Coker 1919
Ellipsaria lineolata	*Plagiola securis*	Utterback 1914; Coker 1919; Grier 1926
	Plagiola lineolata	Grier 1926
Elliptio crassidens	*Unio crassidens*	Coker 1919; Grier 1926
	Elliptio niger	Grier 1926
Elliptio dilatata	*Unio gibbosus*	Danglade 1912; Utterback 1914; Coker 1919; Grier 1926
	Elliptio dilatatus	Grier 1926
Fusconaia ebena	*Quadrula ebena*	Danglade 1912; Utterback 1914
	Quadrula ebenus	Coker 1915; Coker 1919; Grier 1926
	Fusconaia ebena	Grier 1926
Fusconaia flava	*Quadrula rubiginosa*	Wilson and Danglade 1914; Utterback 1914; Coker 1919
	Quadrula subrotunda	Coker 1919
	Quadrula undata	Wilson and Danglade 1914; Coker 1919; Grier 1926
	Fusconaia undata	Grier 1926
Lampsilis abrupta	*Lampsilis orbiculata*	Coker 1919
Lampsilis capax	*Lampsilis capax*	Coker 1919
Lampsilis cardium	*Lampsilis ventricosa*	Wilson and Danglade 1914; Coker and Southall 1915; Utterback 1914; Coker 1919; Grier 1926
Lampsilis fasciola	*Lampsilis multiradiata*	Coker 1919
Lampsilis higginsii	*Lampsilis higginsii*	Coker 1919; Grier 1926
Lampsilis ovata	*Lampsilis ovata*	Coker 1919
Lampsilis siliquoidea	*Lampsilis hydiana*	Coker 1915; Coker 1919
	Lampsilis luteola	Danglade 1912; Wilson and Danglade 1914; Coker and Southall 1915; Coker 1919; Grier 1926
	Lampsilis luteolus	Shira 1913
	Lampsilis siliquoidea	Grier 1926
Lampsilis teres	*Lampsilis anodontoides*	Danglade 1912; Shira 1913; Utterback 1914; Coker 1919; Grier 1926
	Lampsilis fallaciosa	Danglade 1912; Shira 1913; Coker and Southall 1915; Coker 1919; Grier 1926
Lasmigona complanata	*Symphynota complanata*	Wilson and Danglade 1914; Coker and Southall 1915; Coker 1919; Grier 1926
	Lasmigona complanata	Grier 1926
Lasmigona costata	*Symphynota costata*	Wilson and Danglade 1914; Coker 1919; Grier 1926
	Lasmigona costata	Grier 1926
Ligumia recta	*Lampsilis recta*	Utterback 1914; Wilson and Danglade 1914; Coker and Southall 1915; Coker 1919; Grier 1926
	Eurynia recta	Grier 1926
Ligumia subrostrata	*Lampsilis subrostrata*	Coker 1919; Grier 1926
	Eurynia subrostrata	Grier 1926

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Table 2 (*concluded*).

Present nomenclature	Historical nomenclature	Source
Megalonaias nervosa	*Quadrula boykiniana*	Coker 1919
	Quadrula heros	Danglade 1912; Isley 1914; Utterback 1914; Coker 1919; Grier 1926
	Megalonaias heros	Coker 1915; Grier 1926
Obliquaria reflexa	*Obliquaria reflexa*	Shira 1913; Coker 1919; Grier 1926
Obovaria olivaria	*Obovaria ellipsis*	Utterback 1914; Coker 1919; Grier 1926
	Obovaria olivaria	Grier 1926
Obovaria retusa	*Obovaria retusa*	Coker 1919
Obovaria subrotunda	*Obovaria circulus*	Coker 1919
Plectomerus dombeyanus	*Quadrula trapezoides*	Coker 1919
Plethobasus cooperianus	*Quadrula cooperiana*	Coker 1919
Plethobasus cyphyus	*Pleurobema aesopus*	Grier 1926
	Pleurobema aesopus	Coker 1919
	Plethobasus cyphyus	Grier 1926
Pleurobema cordatum	*Quadrula plena*	Coker 1919
Pleurobema plenum	*Quadrula obliqua*	Coker 1919
Pleurobema rubrum	*Quadrula pyramidata*	Coker 1919
	Pleurobema pyramidatum	Grier 1926
Pleurobema sintoxia	*Quadrula coccinea*	Utterback 1914; Wilson and Danglade 1914; Coker and Southall 1915; Coker 1919
Potamilus alatus	*Lampsilis alata*	Wilson and Danglade 1914; Coker and Southall 1915; Coker 1919; Grier 1926
	Proptera alata	Grier 1926
Potamilus purpuratus	*Lampsilis purpurata*	Coker 1919
Ptychobranchus fasciolaris	*Ptychobranchus phaseolus*	Coker 1919
Quadrula cylindrica	*Quadrula cylindrica*	Coker 1919
Quadrula fragosa	*Quadrula fragosa*	Shira 1913; Coker 1919
Quadrula metanevra	*Quadrula metanevra*	Utterback 1914; Coker 1919; Grier 1926
Quadrula nodulata	*Quadrula pustulata*	Shira 1913; Coker 1919
Quadrula pustulosa	*Quadrula pustulosa*	Danglade 1912; Shira 1913; Utterback 1914; Wilson and Danglade 1914; Coker and Southall 1915; Coker 1915; Coker 1919; Grier 1926
Quadrula quadrula	*Quadrula nobilis*	Coker 1915
	Quadrula lachrymosa	Utterback 1914; Wilson and Danglade 1914; Coker and Southall 1915; Coker 1919; Grier 1926
	Quadrula quadrula	Grier 1926
Strophitus undulatus	*Strophitus edentulus*	Wilson and Danglade 1914
Truncilla donaciformis	*Plagiola donaciformis*	Grier 1926
	Amygdalonaias donaciformis	Grier 1926
Truncilla truncata	*Plagiola elegans*	Shira 1913; Coker 1919; Grier 1926
	Amygdalonais truncata	Grier 1926
Tritogonia verrucosa	*Tritogonia tuberculata*	Shira 1913Utterback 1914; Coker 1915; Coker and Southall 1915; Coker 1919; Grier 1926
	Quadrula verrucosa	Grier 1926
Villosa iris	*Lampsilis iris*	Coker 1919

Note: Historic nomenclature was revised to reflect presently accepted unionid taxonomy following Parmalee and Bogan (1998).

provide marked underestimates of mussel age (Anthony et al. 2001). Additionally, in many states, no species-specific size restrictions were enacted for several decades. Mussel species, both large and small, were therefore considered equally productive by the early attempts at protective legislation although it is unlikely that a uniform size restriction across all harvested species would protect all species' pre-reproductive individuals.

In addition to regulatory legislation, efforts to artificially propagate and reintroduce mussels were mounted by the biologists at the Fairport Biological Station to supplement low natural recruitment (Smith 1919). Mussel sanctuaries were established where propagated juvenile mussels were introduced. Although by 1925 some recovery was noted in populations in these sanctuaries (Southall 1925; Grier 1926), it was short-lived as intensive harvests devastated the populations in the years following the end of harvest moratoria (Southall 1925).

Paradoxically, following a report in 1931 that documented commercial harvest as a primary factor involved in mussel declines (Ellis 1931), many restrictions on mussel harvests were lifted (Carlander 1954). Other factors, including the

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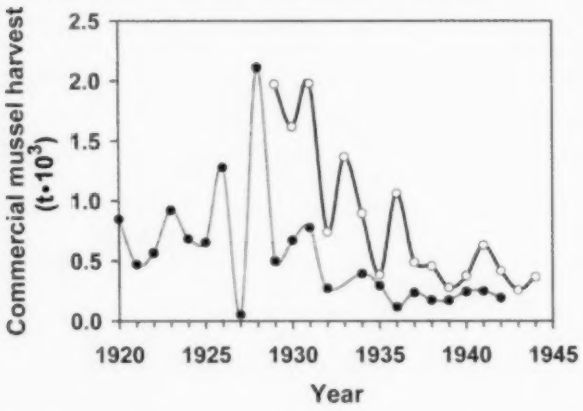
Fig. 6. The trends in freshwater mussel yields (t) of Iowa's Mississippi River fishery (●; gray line) are shown for 1920 to 1942. The trends evident for Iowa's total freshwater mussel catch (○; black line) from 1929 to 1944) show the majority of Iowa's freshwater mussel harvests originated in the Mississippi River fishery. Data are from the Iowa Department of Natural Resources.[2]



construction of the system of navigation locks and dams now present on the Mississippi River, were expected to cause further declines in freshwater mussel populations (Ellis 1931). The U.S. Bureau of Fisheries felt it was of greater value to use up the resource before it was "inevitably" destroyed through environmental degradation (Carlander 1954). Although the removal of restrictions and the rising value of shell should have led to increased harvests, Mississippi River catch statistics from the state of Iowa show that overall, mussels remained in decline (Fig. 6). These decreased harvests even after a relaxation of harvest regulations suggest that commercial mussel stocks were so severely depleted by the early 1930s that lifting harvest restrictions could not augment yields.

Budget constraints at the U.S. Bureau of Fisheries prevented comprehensive surveys of catch statistics from the Mississippi River between 1931 and 1950 (Anderson and Peterson 1953), but statistics for states where data are relatively complete (e.g., Alabama, Arkansas, Illinois, Indiana, Iowa, Kentucky, Tennessee) allow an examination of the patterns and magnitudes of harvests within the Mississippi River Drainage Basin during this period. Although yields in all states exhibit an overall decline through time, the substantial magnitudes and variable nature of harvests are apparent (Fig. 7*a*, 7*b*). Most available catch data are, however, for years following the most extensive mussel harvests and are, in fact, from the period of the button industry's slow demise (Fig. 3).

Although it seems likely, given anecdotal evidence, that mussel stocks were being rapidly depleted throughout the U.S., the correspondence of trends in mussel yields among states suggests that market factors associated with fluctuations in the button production industry's demand for shells, rather than population limitations, were important stimuli to the patterns and magnitudes of annual harvests during 1930–1959 (Fig. 7*a*, 7*b*). The ability of mussel populations to support short-term high commercial harvests despite widespread stock depletion illustrates that these historic beds must have been more extensive and densely populated than today's remnant populations.

The relatively complete catch statistics from the state of Iowa for mussel harvests on the Mississippi River and other smaller Iowa rivers, as well as those of the fisheries of the Great Lakes Drainage Basin, provide further insight into the role of mussel stock depletion in the decline of the button industry. Although harvests in the Mississippi River were important to the Iowa mussel fishery, the significant proportion of harvests from Iowa's inland streams is apparent (Fig. 6). Catch statistics from these smaller inland streams.[2] show that yields peaked near the onset of the button industry's economic decline and exhibited dramatic declines thereafter (Fig. 8). Although the Iowa harvests on the Mississippi River show a similar pattern of decline (Fig. 6), it is notable that the harvests of smaller inland populations fell to near zero decades before those of the Mississippi River. That these declines were occurring despite the fact that increased value of shell probably increased demand for shell indicates overexploitation in these fisheries. Recent surveys of many of the same inland streams corroborate this suggestion because mussel populations have shown no signs of recovery in the five decades following closure of the pearl button industry (K.E. Arbuckle and J.A. Downing, Iowa State University, Ames, Iowa, U.S.A., unpublished data).

Some of the trends of peaks and declines in commercial mussel yields from Iowa's smaller interior streams correspond to those seen in the state-wide harvest statistics and indicate an influence of overall market factors (Fig. 8). The patterns of mussel harvest in Iowa's inland fisheries may not, however, only reflect economic oscillations of a dying button industry. Rather, the alternating patterns of increasing and decreasing yields among some of these inland streams probably indicate patterns of rapid exploitation and depletion of rich mussel beds and their subsequent abandonment for newly discovered or more economical beds on nearby streams (e.g., Fig. 8*a*). This stream-to-stream depletion of mussel stocks is often described in documentation of historical mussel harvests (e.g., Coker 1914, 1919; Smith 1919).

Mussel catch data for the fisheries of the U.S. Great Lakes Drainage Basin also implicate local stock depletion as a major factor influencing the decline of U.S. mussel fisheries (Fig. 9). Even as the value per unit mass of mussels exploited in these fisheries more than doubled, declining mussel harvests made only a weak recovery in 1936 before declining rapidly to near zero in 1940 (Fig. 9). These years of minimal yield preceded the rapid decline in shell value in this fishery that became apparent by the late 1930s (Fig. 9).

Although several have attributed the decline of the American button industry prior to the advent of plastics to the presence of foreign competition and the failure of the U.S. to implement protective tariffs (e.g., Thiel 1981; Claassen 1994; Fassler 1994), it is likely that overexploitation and the reduction in maximal size of marketable shells (Coker 1914, 1919) played a more important role than previously perceived. The lack of large, high-quality shells would have undermined the U.S. industry's ability to suppress competition, allowing the rise of foreign competitors. In fact, foreign competition did not become economically viable until the domestic mussel resource had become depleted. If mussel stocks had not been so dramatically overexploited during the

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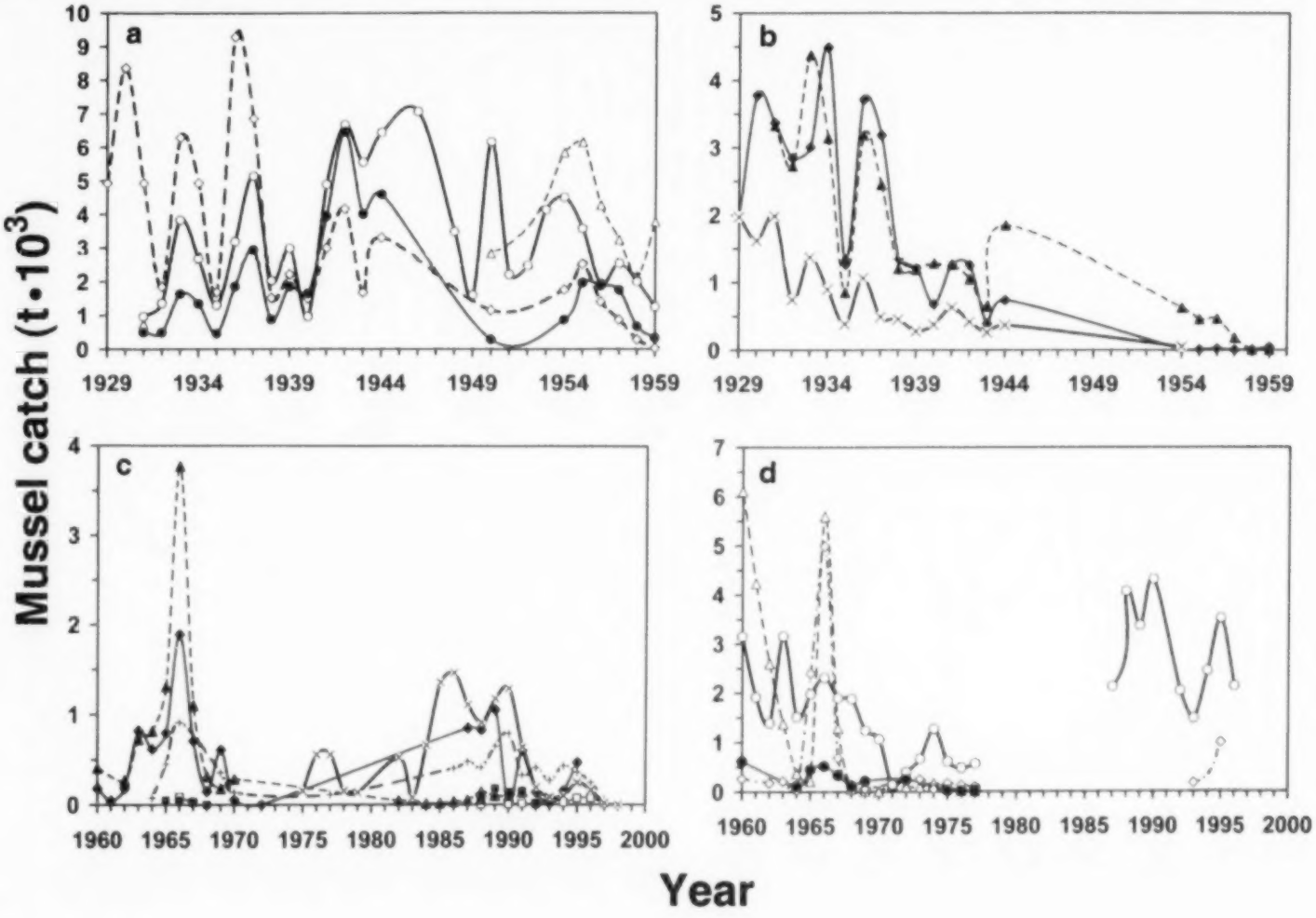
Fig. 7. Mussel harvest trends from freshwater button mussel fisheries in the U.S. states of (*a*) Alabama (△), Arkansas (◇), Tennessee (○), and Kentucky (●). (*b*) Indiana (▲), Illinois (◆), and Iowa (×) show substantial fluctuations between 1929 and 1959. Harvest trends from freshwater mussel fisheries in (*c*), the midwestern U.S. states of Illinois (◆), Indiana (▲), Minnesota (□), Missouri (■), Wisconsin (+), and Iowa (×) show substantial fluctuations between 1960 and 1998 as do trends from (*d*) Alabama (△), Arkansas (◇), Tennessee (○), and Kentucky (●) for harvests between 1960 and 1996. Data are from Fiedler (1931, 1932, 1936*a*, 1936*b*), Fiedler et al. (1936), Fiedler (1938, 1940*a*, 1940*b*, 1941), Brann (1947), Anderson and Peterson (1953), Anderson and Power (1956, 1957), Power (1958, 1959, 1960, 1961, 1962, 1963), Power and Lyles (1964), Lyles (1965, 1966, 1967, 1968, 1969), Stans (1971), Wheeland (1972, 1973), Thompson (1974), Wheeland (1975), Pileggi and Thompson (1976), Wise and Thompson (1977), Pileggi and Thompson (1978, 1980), Thompson (1984), Koch (1991, 1992, 1993), Todd (1993), the Iowa Department of Natural Resources,[2] and the Wisconsin Department of Natural Resources (K. Welke, Mississippi River Fisheries Management Office, unpublished data).



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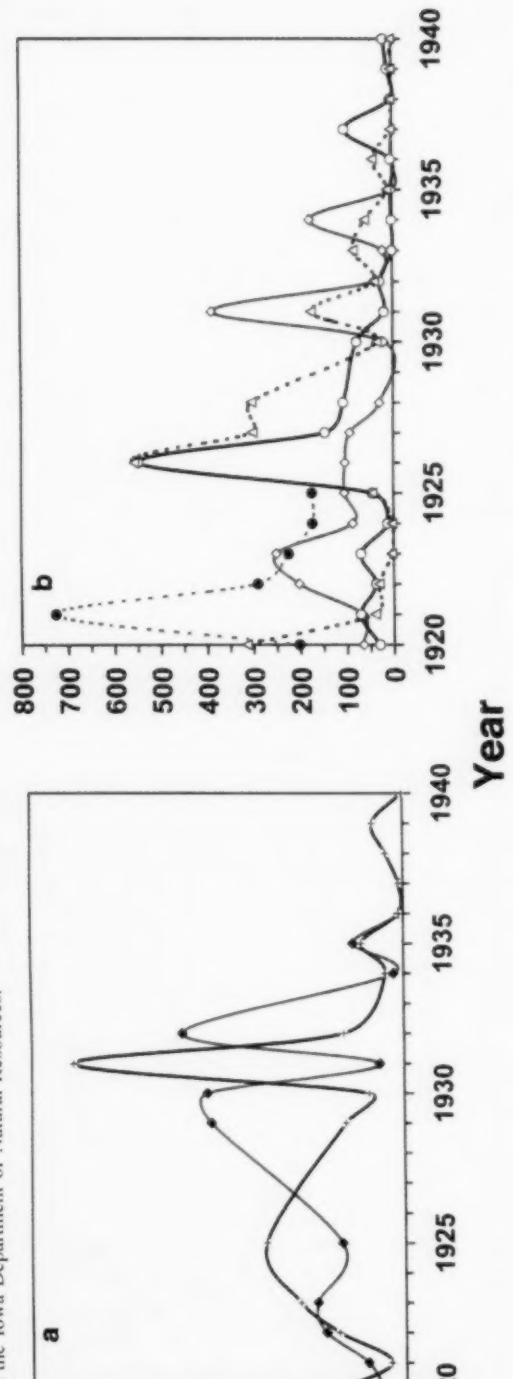

Fig. 8. The trends in freshwater mussel yields (t) for (*a*) Iowa's Skunk River (+; black line) and Iowa River (◆; gray line); (*b*) the Des Moines River (◇; solid gray line), the Wapsipinicon River (○; solid black line), the Shell Rock River (●; broken gray line), and the Cedar River (△; broken black line) fluctuated dramatically between 1920 and 1940. Data are from the Iowa Department of Natural Resources.[2]

freshwater pearl rushes and early after the button industry's onset, a larger standing supply of cheap available domestic shell material would have allowed the U.S. freshwater button industry to stifle foreign competitors and maintain a dominant economic presence until the advent of inexpensive plastics or the depletion of these large standing stocks.

Cultured-pearl industry: 1950–present: history and development of the industry

The third and most recent bout of intensive freshwater mussel exploitation in the U.S. has provided the raw material for the Asian cultured-pearl industry. A veil of secrecy surrounds this multi-billion-dollar (1998 $U.S.) industry to preserve monopolistic controls. This generally precludes an extensive synopsis of the industry, however, and literature is consequently quite limited (Fassler 1991).

As early as 1904, the Japanese were experimenting with the production of cultured pearls using artificial nuclei (Fassler 1994). It was soon discovered that when spherical beads created from the shells of freshwater mussels (Fig. 10) were placed into an incision in the tissue of a marine pearl oyster (a process called grafting), they served as exceptional nuclei as the oyster surrounded the beads with nacreous secretions (Fassler 1991). Information regarding the grafting process and the technology involved has, until recently, been closely guarded to ensure Japan's place as the world's sole producer of high-quality cultured pearls (Ward 1985; Fassler 1991, 1994).

The world's rapid acceptance of the new cultured pearls accelerated the development of the industry. By 1934, Japanese pearl farmers had nucleated over 15 million oysters (Fassler 1994), and in 1938, they produced over 11 million pearls (Claassen 1994). Although cultured-pearl farms gradually spread throughout many of the South Pacific atolls, Japan remained in control of the labor, technology, and a majority of the exports even outside of its own borders (Fassler 1991). In 1985, some individual pearls from these South Sea nations were valued at between $6000 and $60 000 (1998 $U.S.) (Ward 1985). By 1990, the expansive industry produced pearls worth over $1.1 billion (1998 $U.S.) (Fassler 1991), and presently the cultured-pearl industry employs hundreds of thousands worldwide and boasts retail sales exceeding $3 billion (1998 $U.S.) annually (Hubbs and Jones 1996).

Although Chinese shell material was the mainstay of the Japanese industry in the early days of the cultured-pearl industry, U.S. shell became the sole source of nuclei by the 1950s (Neves 1999). Japan's monopolistic control over the industry began to deteriorate with the depletion of freshwater mussel stocks in the U.S. and pollution-related mortality of the pearl oysters in Japan (Claassen 1994; Fassler 1994; Neves 1999). As American mussel stocks are dwindling, the economic viability of the cultured-pearl industry and the U.S. mussel fisheries are waning. The search for artificial nuclei to substitute for American shell has begun (Fassler 1994), prompting many to suggest that the most recent commercial market for U.S. freshwater shell has begun to dissolve (e.g., Claassen 1994; Fassler 1994). Others are optimistic (Neves 1999), and markets outside of Japan are expanding (Fassler 1994). Just as in the freshwater pearl and button industries, however, foreign competitors and alternative

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resources became economically viable only after substantial depletion of the American mussel resource.

Mussel harvests and conservation during the cultured-pearl era

As mussel harvests for the production of pearl buttons dwindled, U.S. freshwater mussel fisheries were revived by the cultured-pearl industry. As early as the 1920s, U.S. shell exports to Japan, composed primarily of *Fusconaia* and *Pleurobema* species, had grown large. Because it requires up to 30 kg of shells to produce a single kilogram of nuclei, the growing cultured-pearl industry demanded a substantial supply of North American shells (Claassen 1994; Fassler 1994). Exports that near the industry's onset consisted solely of raw shell saw the gradual inclusion of nuclei manufactured in the U.S. In 1968, U.S. shell exports exceeded 22 000 t annually (Claassen 1994), and by the early 1990s, shell exporting was a 70-million-dollar per year industry (Ahlstedt and McDonough 1993). Despite its substantial magnitude, the value of the U.S. shell export industry remains far below that of the pearl button industry at its peak (cf. Fig. 3).

A majority of the early mussel harvests for the cultured-pearl industry consisted of *Fusconaia* and *Pleurobema* species from the Tennessee River, which pearl producers had deemed of the highest quality for nucleus production. In 1960, the nearly 900 Tennessee River musselers netted over $1 250 000 (1998 $U.S.) and, by 1962, musselers on the same stream could expect daily catches of 180 kg·person^{-1} (Claassen 1994). In spite of technologically advanced harvest methods (e.g., SCUBA, etc.), these daily takes, although substantial, were far below many historical daily catches obtained with more primitive methods (cf. Fig. 5) and the mussel resources of the Tennessee River soon became exhausted (Ahlstedt and McDonough 1993). Consequently, pearl producers began to accept increasingly larger harvests from a growing number of streams. In 1965, for example, harvests on the Wabash River peaked at over 900 t (Anderson et al. 1993) and this stream became one of the most important mussel fisheries in the U.S. (Fig. 11).

The pursuit of new fishing grounds could not stave off declining yields for long, however. Mussel resources in some of the most productive U.S. streams, including the Tennessee and Wabash Rivers, were showing signs of exhaustion (Fig. 11). Mussel densities had been declining since 1965 in the Upper Mississippi River (Thiel 1981). Mass die-offs were also becoming more common in some streams (Todd 1993; Claassen 1994) including one event that impacted mussel populations throughout an extensive stretch of the Mississippi River north of Keokuk, Iowa (Thiel and Fritz 1993).

Faced with the exhaustion of marketable shell stocks, pearl producers, just as the button manufacturers before them, began to accept more species to ensure that the desired supply of shells and nuclei could be satisfied. The washboard, *Megalonaias nervosa*, became the most valuable commercial species (Fassler 1994). Presently, at least 21 unionid mussel species, five of which are considered species of special concern (Williams et al. 1993), have some commercial value (Table 3). Nevertheless, marketable mussel stocks continued to decline as demand for shell increased.

Despite the decline in availability of marketable shell stocks, the rising value of shell allowed increases in fishing effort through the 1980s and into the 1990s in many states (Crowell and Kinman 1993). In 1991, the state of Tennessee alone supported over 2300 musselers (Todd 1993). The classical signs of overexploitation noted previously during harvests for pearl button production have again become evident in many U.S. mussel fisheries. For example, Thiel (1981) noted that previously valuable mussel beds in the Upper Mississippi River could not support musseling by the late 1970s. Mussel populations in Kansas have experienced a nearly 10-fold reduction in density since the 1960s (Busby and Horak 1993). Consequently, increasing shell value has allowed musselers to turn to previously uneconomical or unexploited beds to support annual harvests (Anderson et al. 1993). Recent accounts of commercial exploitation also note increased occurrences of illegal harvesting activity (e.g., Anderson et al. 1993; Hubbs and Jones 1996; Whitney et al. 1997).

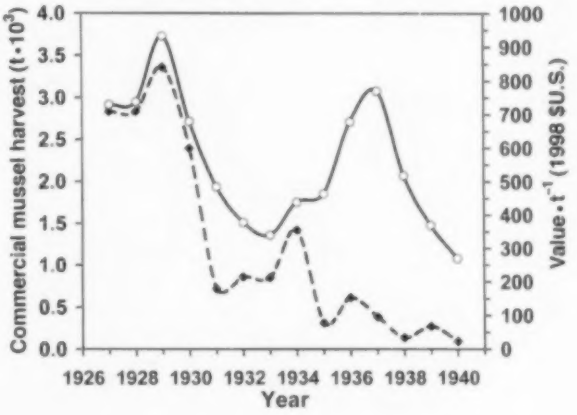

Fig. 9. Trends in commercial mussel yields (t) (◆) for the Great Lakes Drainage Basin show wide fluctuations between 1927 and 1940. While yields declined dramatically beginning in 1929, value·t^{-1} (1998 $U.S.) (○) began to increase in 1933 before again declining in 1937. Data are from Radcliffe (1927), Fiedler (1931, 1932, 1936*a*, 1936*b*), Fiedler et al. (1936), and Fiedler (1938, 1940*a*, 1940*b*, 1941).

A further indication of substantial overexploitation is that large, valuable individual mussels are absent from many fisheries despite a lucrative economic incentive for their harvest (Hubbs and Jones 1996; Neves 1999). Quantitative surveys of exploited populations also suggest that few individuals of commercially valuable species larger than the minimum legal size exist in many fisheries (e.g., Whitney et al. 1997). Even when animals do reach minimum legal size, they are quickly harvested. The decline in abundance and size of the most valuable mussel species has often prompted musselers to shift their effort to smaller individuals of less valuable species to supplement their harvests (Hubbs and Jones 1996; Neves 1999). Just as in mussel fisheries for button production, the trend toward growth overfishing is apparent.

As evident in catch statistics for the button industry, the similarities in the trends in more recent catch statistics of U.S. midwestern mussel fisheries (Fig. 7*c*), and to a lesser degree, those of southern U.S. states (Fig. 7*d*) may be indicative of market trends driving commercial harvests. Closer

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Fig. 10. Round beads, or nuclei, are presently created from the shells of U.S. freshwater mussels and exported for use in the cultured-pearl industry. Nuclei are shown here below one of the currently most commercially valuable freshwater mussel species, the washboard, *Megalonaias nervosa*. Nuclei were provided by C. Lawson, Empire Shell Products, Garnavillo, Iowa. Photo by J.L. Anthony.

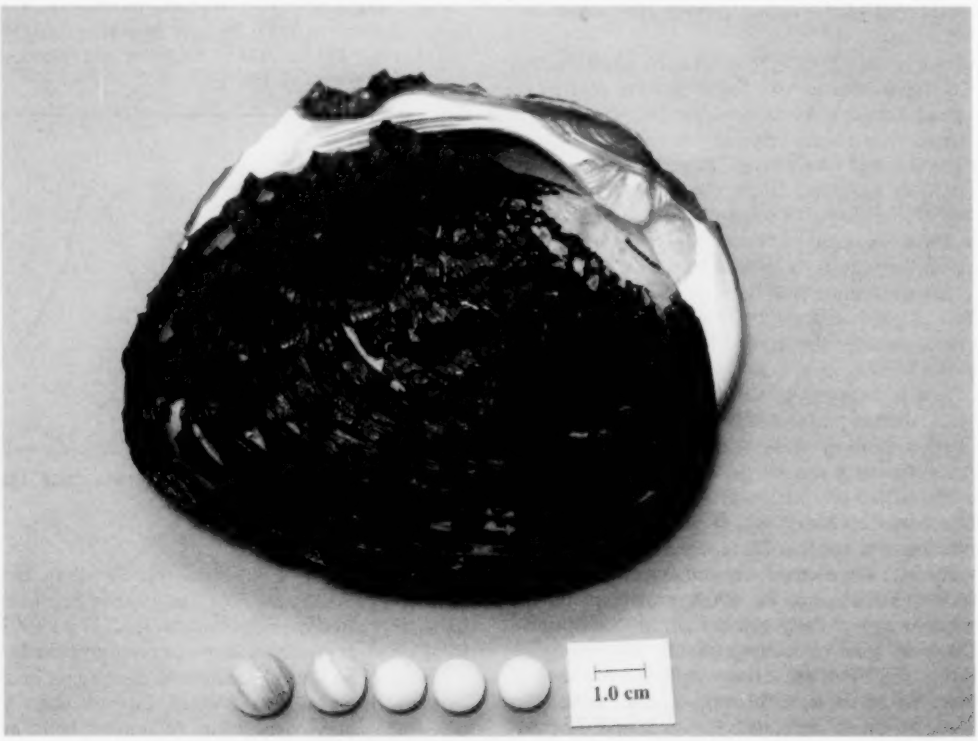
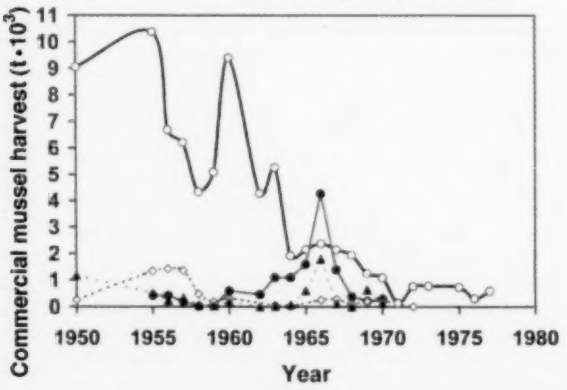


Fig. 11. Commercial harvest trends for major U.S. mussel fisheries on the Tennessee (○), Wabash (●), Ohio (◇), and Mississippi (▲) rivers show overall declines through time. Data are from Anderson and Peterson (1953), Anderson and Power (1956, 1957), Power (1958, 1959, 1960, 1961, 1962, 1963), Power and Lyles (1964), Lyles (1965, 1966, 1967, 1968, 1969), Stans (1971), Wheeland (1972, 1973), Thompson (1974), Wheeland (1975), Pileggi and Thompson (1976), Wise and Thompson (1977), Pileggi and Thompson (1978, 1980), and Thompson (1984).



examination of Iowa's Mississippi River mussel fishery with its relatively complete data, however, also seems to implicate overexploitation in recent declines in mussel yields. Following a peak year in 1986 (1464 t), commercial mussel yields in Iowa's Mississippi River have declined precipitously to less than 0.5 t in 1998 (Gritters and Aulwes 1998).

Data from the Iowa Department of Natural Resources[2] show that the value·t^{-1} of shells increased from just over $1000 (1998 $U.S.) in 1987 to over $3500 (1998 $U.S.) by 1994 (Fig. 12*a*). Meanwhile, the yields of the fishery were declining (Fig. 7*c*). Had mussel populations been healthy and capable of sustained exploitation, increases in harvests should have been observed given the high value of the shells and the high demand for shell exports. Even while shell values were rapidly increasing, however, effort was generally decreasing (Gritters and Aulwes 1998). Catch per unit effort (CPUE) also decreased substantially from 52 kg·diver hour^{-1} in 1987 to 10 kg·diver hour^{-1} in 1998 (Fig. 12*a*). Thus, if density is proportional to CPUE, mussel abundance within dwindling mussel beds probably declined more than fivefold in a decade. An additional consideration is that, in Iowa, Illinois, and Wisconsin, dead shells (possibly remnants of a mid-1980s die-off in the Upper Mississippi River) composed a significant proportion, and in some years, the majority of the total yield of the most highly sought mussel species, *M. nervosa* (Thiel and Fritz 1993).

Iowa's mussel fishery was not the only fishery in significant decline by the late 1990s. Even the extensive mussel fisheries in the state of Tennessee, which often yield up to 50% of the total U.S. catch (Hubbs and Jones 1996), are characterized by declining indices of CPUE since the early

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Table 3. At least 21 North American freshwater mussel species presently have some commercial value for the production of nuclei for cultured pearls.

Species	Source
Actinonaias ligamentina	Anderson et al. 1993
Amblema plicata	Koch 1992; Ahlstedt and McDonough 1993; Anderson et al. 1993; Busby and Horak 1993; Crowell and Kinman 1993; Todd 1993; Hubbs and Jones 1996; Gritters and Aulwes 1998
Cyclonaias tuberculata	Ahlstedt and McDonough 1993; Anderson et al. 1993; Todd 1993
Ellipsaria lineolata	Ahlstedt and McDonough 1993
Elliptio crassidens	Ahlstedt and McDonough 1993; Anderson et al. 1993; Todd 1993
Fusconaia ebena	Todd 1993; Hubbs and Jones 1996
Fusconaia flava	Anderson et al. 1993; Busby and Horak 1993; Todd 1993; Hubbs and Jones 1996; Gritters and Aulwes 1998
Lampsilis cardium	Busby and Horak 1993
Obovaria olivaria	Anderson et al. 1993; Gritters and Aulwes 1998
Megalonaias nervosa	Koch 1992; Ahlstedt and McDonough 1993; Anderson et al. 1993 Crowell and Kinman 1993; Todd 1993; Hubbs and Jones 1996
Obliquaria reflexa	Ahlstedt and McDonough 1993
Pleurobema coccineum	Busby and Horak 1993
Pleurobema cordatum	Ahlstedt and McDonough 1993; Todd 1993
Potamilus alatus	Ahlstedt and McDonough 1993; Gritters and Aulwes 1998
Potamilus purpuratus	Busby and Horak 1993
Quadrula asperata	Hubbs and Jones 1996
Quadrula metanevra	Anderson et al. 1993; Busby and Horak 1993; Todd 1993; Gritters and Aulwes 1998
Quadrula nodulata	Todd 1993
Quadrula pustulosa	Ahlstedt and McDonough 1993; Anderson et al. 1993; Busby and Horak 1993; Gritters and Aulwes 1998
Quadrula quadrula	Koch 1992; Ahlstedt and McDonough 1993; Anderson et al. 1993; Busby and Horak 1993; Crowell and Kinman 1993; Todd 1993; Hubbs and Jones 1996; Gritters and Aulwes 1998
Tritogonia verrucosa	Ahlstedt and McDonough 1993; Anderson et al. 1993

1970s (Fig. 12*b*). Likewise, indices of CPUE declined in Wisconsin's mussel fisheries beginning in the late 1980s (Fig. 12*c*).[4] These fisheries all indicate a consistent near-fivefold decline over the periods plotted. Mussel stocks may be dangerously depleted in these and other U.S. fisheries.

Many reasons have been suggested to explain these most recent mussel declines. The harmful effects of the invasion of the exotic zebra mussel are often considered one of the primary factors leading to the decline of U.S. mussel fisheries (Thiel and Fritz 1993; Fassler 1994). It is interesting to note, however, that zebra mussels became well established in the Mississippi River Basin between 1991 and 1993 (Fassler 1994). Many fisheries in the Mississippi River watershed were, at this point, already in significant decline (Fig. 7*c*, 7*d*) and characterized by declining CPUE (Fig. 12). Although zebra mussels are certainly impacting unionid mussels, it appears that unionid mussel populations were already declining in the midwestern U.S. when they arrived.

Some of the declines in harvests and CPUE may also be the result of a tightening of restrictions, including higher licensing fees and larger minimum legal size limits, on the mussel fisheries in 1979, 1987, and during the 1990s (Thiel and Fritz 1993; Todd 1993; Gritters and Aulwes 1998). Increases in minimum legal size have generally been small, however, and as noted by Neves (1999), the value of even considerably more expensive licenses may be recovered in as little as one day of harvest. Furthermore, these recently imposed regulations may be too little, too late. For example, many of the states along the Upper Mississippi River had no species restrictions enacted before 1979, over 80 years after the first extensive mussel harvests began (Thiel and Fritz 1993). Restrictions in maximum size limits have also remained insufficiently small (Thiel and Fritz 1993) and static for decades (Busby and Horak 1993; Crowell and Kinman 1993; footnote 4) despite widespread stock depletion. Daily catch limits are also nonexistent in most states (e.g., Busby and Horak 1993; Thiel and Fritz 1993; footnote 4). Although declining yields may also be partly due to a recent decline in Japanese demand for shell (Neves 1999), there is evidence that after over a century of overexploitation and decline American freshwater mussel stocks are simply not able to support extensive exploitation.

Conclusion

Although quantitative analyses of freshwater mussel populations prior to 1900 are rare and few continuous data sets of mussel fishery statistics exist, our analysis points to substantial overexploitation as a primary contributor to the decline of mussel fisheries in the U.S. Declines in CPUE and likely harvestable mussel stocks, demonstrate a serious level of resource degradation. Furthermore, declining maximum sizes and the fact that few mussels over the minimum legal size exist suggest an overly intense level of exploitation. Both historic and recent trends in mussel fisheries have implied that unionid mussels do not support a sustainable intensive fishery even under favorable market conditions. In fact, declining indices of CPUE and yields imply that mussel populations are now incapable of supporting a sustainable fishery at levels of harvest far below those historically extracted. Knowledge of the ecology of these declining mussel

[4] K. Welke, Wisconsin Department of Natural Resources, Mississippi River Fisheries Management Office, 315 East Cedar, Prairie du Chien, WI 53821, U.S.A., unpublished data.

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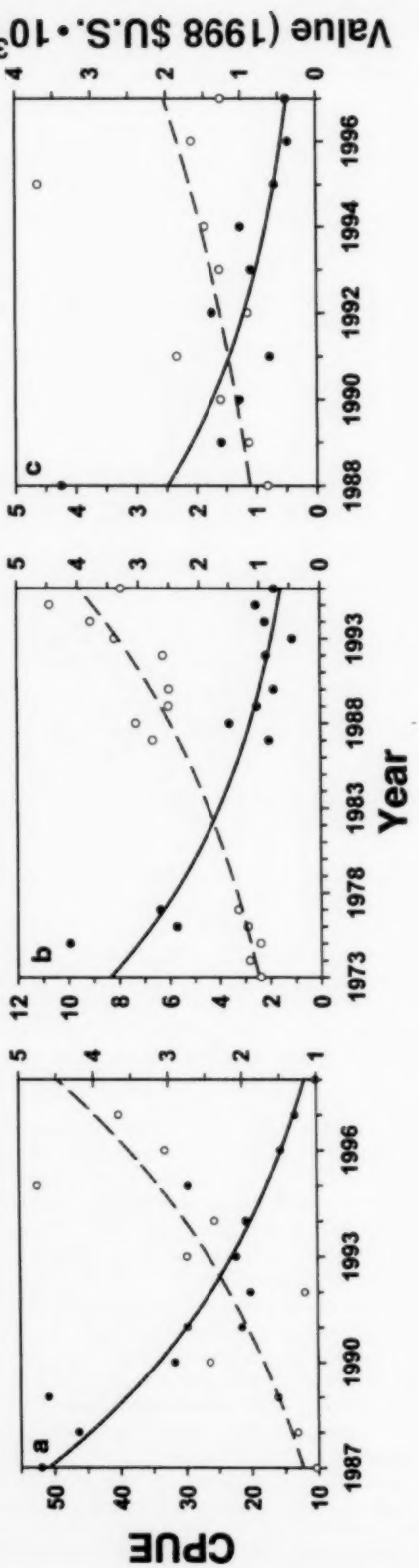

Fig. 12. CPUE (diver hours) for (*a*) Iowa's Mississippi River freshwater mussel fishery (kg·diver hour^{-1}) (●; solid black line) show dramatic declines through the mid-1980s to 1998 as shell values (1998 $U.S.·10^3·t^{-1}) (○; broken gray line) increase. Indices of CPUE (t·license^{-1}) (●; solid black line) and shell values (1998 $U.S.·10^3·t^{-1}) (○; broken gray line) for (*b*) Tennessee (1973–1996) and (*c*) Wisconsin (1985–1998) generally decline through time. Data are from Wise and Thompson (1977), Pileggi and Thompson (1978, 1980), and Thompson (1984), Todd (1993), and Hubbs and Jones (1996), Gritters and Aulwes (1998), and the Wisconsin Department of Natural Resources.[4]

species must be improved before mussel conservation and fishery management can be based upon adequate knowledge of these sparse and jeopardized populations.

This analysis of American mussel fisheries offers more than a means of understanding the present state of U.S. mussel populations, however. This resource trajectory is especially interesting to managers of other resources since it has been played out in almost a complete regulatory vacuum, therefore illustrating the long-term impacts of "regulation" by nearly pure market forces. It is rare that we are offered the chance to examine more than a century of the history of a group of biological resource organisms. Analysis of the history of freshwater mussel fisheries can therefore help us to contemplate the future of this and other exploited organisms. Several general conclusions emerge when the long record is assembled from these many disparate sources. Although these general lessons are not all new, they emerge clearly from this long record, and are of likely relevance to resources with shorter or less developed historical data.

Nine general lessons learned from the mussel fisheries

1. Short-term economic decisions can impede long-term resource sustainability

Exploitation regulated principally by short-term economic decisions by free entrants to the harvest arena can engender long-term resource impacts. This is because long-term sustainability has no economic relevance to those drawn to a resource by the potential for short-term monetary gain. This is most profoundly illustrated by the exhaustive harvests during the pearl rushes but is also illustrated by substantial declines in CPUE during the button and cultured-pearl nucleus eras, as well as current extensive poaching of endangered populations. Overexploitation at each stage decreased profitability of the subsequent industry.

2. Basic biology and ecology sets the upper limits for harvest intensity

Knowledge of the basics of growth, reproduction, density dependence and population dynamics must be known to estimate biological production and model renewal under exploitation scenarios. Despite over a century of commercial interest in freshwater mussels, however, even basic aspects of their growth, longevity, and population ecology are poorly known (e.g., Anthony et al. 2001; Strayer and Ralley 1993). The apparent inability of contemporary yields to approach historic magnitudes illustrates that intensive harvest in the absence of this knowledge has led to decline and near extinction of the mussel resource base. It is also possible that some classes of organisms may not reproduce or grow in the way predicted by classical fisheries management theory and may be incapable of sustained exploitation. This is not new to management theory, but the mussel industry offers yet another profound example of the impact of violating this rule.

3. Loss of exploited populations depends on the rate of harvest relative to the rate of production

Seemingly inexhaustible resources can disappear in a short time if their production intervals are long relative to the rate of harvest. This is especially clear in freshwater mussels because they were observed at near legendary densi-

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ties early in the 20th century, but long lives and slow growth (e.g., Anthony et al. 2001) mean that they renew themselves very slowly. During the button and cultured-pearl industries, long-lived declines in yields after short-term high magnitude harvests illustrate the rapid exhaustion of large standing stocks, followed by negligible recovery.

4. Delays in resource management and regulation may be dangerous to resource viability

The danger signs of overexploitation should be followed rapidly with regulations to sustain the resource. In mussel fisheries, calls for regulation were ignored until decades after the onset of harvests. Even short time lags in enforcement of regulations due to short-term funding shortfalls can have long-term consequences, however. An example of this is the U.S. Bureau of Fisheries funding shortfall from the 1930s–1950s. These financial problems precluded the collection of data that would have shown extreme depletion of the mussel fauna during this period. In any case, decade-scale declines in resources should be taken as an immediate indication of a need for stringent and decisive regulation of biological resources. If management has been delayed too long, post hoc regulation (e.g., the current mussel regulation scenario) can be inadequate to restore a resource, perhaps only managing the speed of its decline to extinction.

5. Declining economic viability does not predict future resource uses

The need for conservation of a resource or its restoration cannot be denied because a resource shows current low economic viability. First, the low economic viability itself can result from overexploitation and low yields. Second, future exploitation opportunities and uses are intrinsically unpredictable. For example, pearlers could not foresee the button industry, and button manufacturers could not foresee the demand for cultured-pearl nuclei. Each successive industry would have been more lucrative and had longer-term viability if the preceding industry had managed the resource more carefully.

6. Poor resource management favors competitors

Overexploitation and poor management of domestic supplies of a resource can render foreign competitors and other substitute supplies viable. Declining mussel populations, coupled with labor disputes, probably intensified Japanese competition in the U.S. button market by undermining the American industry's competitive advantage in low-grade button production. As mussel populations continued to decline, the increasing price of pearl buttons probably fueled the switch to synthetic production. Likewise, the low rate of supply of pearl nuclei is favoring Chinese nuclei and research to find synthetic substitutes. At first sight, though, it may appear that declining economic yields are due to competing products when the competing products might not have been viable had the resource been sustained at healthier levels.

7. Overexploited resource yields show unpredictable behaviors

In an unregulated resource arena, the final stages of exploitation may show wild oscillations in yields owing to the discovery and intensive harvest of vestigial patches of declining resource populations or communities. Overexploited resources offer low profitability especially where substantial industrial investment implies high fixed costs (i.e., the rapid capitalization of the pearl button and cultured-pearl industries). In the pearl button arena, rapidly declining yields of traditional beds led to short-term exhaustive removal of mussels from some newly discovered patches, especially in smaller rivers and remote locations. Further, industries tend to press for relaxed regulations when yields are low to help them survive until higher yields return. In the mussel fisheries, rapid alterations of regulations may have caused large variations in overall yields.

8. Intensive harvest of overexploited resources degrades population renewal potential

Unless a substitute product is found early in the exploitation trajectory, economic forces tend to automatically push stocks to extreme low levels with restricted species composition and weak renewal potential. In mussel fisheries, harvest of overexploited populations led to progressive decreases in density, size, and biodiversity as prices rose due to resource rarity. Rising resource value stimulates exploitation, which intensifies degradation. In fact, little recovery of overexploited mussel populations has been documented and it is no surprise that yields during the recent cultured-pearl industry have not matched those noted historically.

9. Intensive harvest can lead to progressive reductions in biodiversity

The sequential depletion and abandonment of rich populations or substocks, noted through the duration of the American mussel fisheries, may mask the true magnitude of metapopulation decline. This leads to abrupt declines of fisheries yields only after many substocks have been driven to commercial extinction. Additionally, when managing a multispecific fishery, failing to track specific population trends may lead to the gradual extermination of less productive species (Clark 1990). This is apparent in the current imperiled status of many formerly exploited mussel species as well as in the continuous shifts of fishing effort among species that were necessary to maintain harvests at the magnitude demanded by industry.

The collapse of the American freshwater mussel fishery mirrors those of many pelagic and demersal fisheries in both fresh and marine waters. The lessons learned from this century-long exploitation trajectory of the declining American mussel fauna must be applied to fisheries management if sustainable fisheries are to persist into the future. As global demand for fisheries products continues to increase, it will be imperative that fisheries be closely monitored and sensibly managed. Failure to act quickly and decisively to protect declining stocks will increase the likelihood of fisheries collapses, limit the potential for long-term fisheries sustainability, and degrade the future value of our aquatic resources.

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Can fisheries yield be enhanced by large-scale feeding of a predatory fish stock? A case study of the Icelandic cod stock

Björn Björnsson

Abstract: The concept of large-scale feeding of a predatory fish stock by natural prey species is introduced and evaluated for the Icelandic cod (*Gadus morhua* L.) stock. The paper addresses the question of whether fisheries yield can be enhanced by relocating food supply in an ecosystem from areas of surplus prey abundance to areas where predator abundance is high and prey abundance low. The benefits of large-scale feeding may be threefold. First, it may increase the growth rate and yield of a predatory fish stock. Second, it may reduce predation on valuable species. Third, it may lower the cost of fishing. For large-scale feeding to be economically feasible it is necessary to have access to large quantities of inexpensive and high-quality feed. In Iceland about 1 000 000 t of capelin, herring, and blue whiting are landed annually for fishmeal production, their price being less than 10% of that of cod. For much of the year these stocks are outside the distributional area of the Icelandic cod stock. The most cost-effective feeding technique must involve purse seiners and pelagic trawlers transporting their catch directly to the feeding locations. Different feeding scenarios, harvesting techniques, and ecological consequences are considered for the Icelandic cod stock.

Résumé : On trouvera ici la proposition du concept de l'alimentation à grande échelle d'un stock de poissons prédateurs au moyen d'espèces de proies naturelles et son évaluation dans le cas du stock islandais de morues (*Gadus morhua* L.). La question est de savoir si on peut augmenter le rendement d'une pêche commerciale en déplaçant les sources de nourriture dans un écosystème, de régions où l'abondance des proies est excédentaire vers des régions où la densité des prédateurs est élevée et celle des proies réduite. Les bénéfices d'une telle alimentation à grande échelle peuvent être de trois ordres. D'abord, elle peut augmenter le taux de croissance et le rendement d'un stock de poissons prédateurs. Ensuite, elle peut réduire la prédation sur une espèce de grande valeur. Finalement, elle peut diminuer le coût de la pêche. Pour qu'une telle alimentation à grande échelle soit rentable sur le plan économique, il faut un accès à de grandes quantités de nourriture peu coûteuse et de haute qualité. En Islande, environ 1 000 000 t de Capelan, de Hareng et de Poutassou sont capturées chaque année pour la production de farine de poisson et leur valeur équivaut à moins de 10% de celle de la morue. Pendant une grande partie de l'année, ces stocks se situent hors de la zone de répartition du stock islandais de morues. La technique la plus rentable consisterait à ce que des bateaux munies de sennes coulissantes et des chalutiers pélagiques transportent directement leurs captures aux sites d'alimentation. On trouvera aussi, pour le stock de morues d'Islande, une discussion de divers scénarios d'alimentation, de différentes techniques de récolte et des conséquences écologiques.

[Traduit par la Rédaction]

Introduction

People have harvested fish and invertebrates from the sea for centuries and the demand for seafood has increased with the growing human population. In recent years about 30% of the global fish catch of 96 000 000 t has been used for fishmeal production (Naylor et al. 2000). It has been argued that much of the increasing demand for fish for direct human consumption can not entirely be met by expanding fisheries and that the gap must be filled by aquaculture.

The development of finfish farming in the sea is, however, limited to relatively few expensive species due to the high cost of cultivation. Large investments are required to build hatcheries and on-growing facilities and the cost of feed and labour is high. A feasibility study suggested that with the current prices of cod it was not economically feasible to grow cod (*Gadus morhua* L.) in Iceland by traditional cultivation methods, either in sea pens or in land-based facilities (Knútsson 1997). Research and development is now underway in Norway, Scotland, Canada, and Iceland to investigate the potential of cod farming.

Large-scale releases of cod juveniles in a fjord on the west coast of Norway did not result in a noticeable increase in cod abundance one year after the release (Smedstad et al. 1994; Nordeide et al. 1994). Apparently there was little or no excess carrying capacity in the Norwegian fjords where the cod juveniles were released (Blaxter 2000). Large-scale releases of juvenile cod in an exposed coastal area in western Norway (Otterå et al. 1999) and on an offshore bank in the Faroe Islands (Fjallstein et al. 1996) also gave low returns.

Experimental feeding in Stödvarfjördur, a small fjord on the east coast of Iceland, resulted in a large increase in the growth rate of free-ranging cod in the feeding area. The growth in gutted weight of the conditioned cod was approxi-

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mately double that of the wild cod receiving no additional feed (Björnsson 1999*a*). During the 17-month feeding experiment in Stödvarfjördur, a total of 100 t of feed was dispensed. However, such a feeding operation cannot be economically viable unless carried out on a much larger scale (Knútsson 1997).

Technological advances in fisheries have been rapid: fishing vessels and catching equipment have improved; less manpower and fewer ships are required to take the catch; stock assessment and fisheries management have improved; in many cases fishing-gear regulations and area closures have reduced by-catch, and; the quota-system has decreased the cost of fishing. Yet, fisheries yield is limited by the productivity of the fish stocks and the maximum sustainable yield is set by the carrying capacity of the environment.

The main purpose of this paper is to raise the question of whether fisheries yield, in terms of net economic value, can be increased by large-scale feeding of a predatory fish stock. The Icelandic cod stock is taken as an example to explore how the idea of large-scale feeding could be implemented. This revolutionary idea must be introduced thoroughly to the scientific community, research authorities, the fishing industry, and the public before enough support can be mounted to test it properly in the field. The necessary ecological experiment must involve cooperation between many scientists using an interdisciplinary approach and advanced technology. Such an ecological experiment may not only be of economic but also of scientific interest. It is hoped that this idea will receive enough attention from the scientific community to initiate such action.

The idea

Large-scale feeding of a top predator in a marine ecosystem to increase the economic yield appears to be a new concept. Similar ideas have been introduced previously for smaller ecosystems. For example, some form of supplementary feeding is carried out in semi-extensive aquaculture in lagoons and freshwater ponds (e.g., in farming of shrimp, tilapia, and carp), to increase yields. Moreover, fish juveniles conditioned to feed at a given sound signal have been released into a coastal area: red sea bream (*Pagrus major* (Temminck and Schlegel)) off the coast of Japan (Fujiya et al. 1980) and cod in a Norwegian fjord (Midling et al. 1987). Sound signals and supplementary feeding were used to keep the free-ranging fish within the area of release. In both cases hatchery-reared juveniles were released into a feeding area, whereas the idea of large-scale feeding presented here relies instead on feeding the wild fish that are already there, i.e., relying on the natural recruitment of the stock.

In sea ranching, hatchery-produced juveniles are released into an area without any supplementary feeding and the success of the operation depends on whether there is excess carrying capacity in the area. Furthermore, successful transplantation depends on removing wild juveniles from an area where food supply is restricted to an area with surplus food supply (Blaxter 2000). Large-scale feeding, on the other hand, involves relocating the food supply in the ecosystem from areas of surplus prey abundance to areas where predator abundance is high and food supply low. In marine ecosystems, where distances are great, the distributions of a predatory species and its prey can differ widely in time and space, which may limit the growth rate and production of the predatory stock. The paper addresses the question of whether this limitation can be overcome by large-scale feeding of the predator.

Many fishing nations have a long tradition of harvesting pelagic fish for the fishmeal industry. There is little or no demand for these fish for direct human consumption and the fishmeal is used as an ingredient in compound feeds for livestock and farmed fish. Usually these pelagic fish species are important prey for larger and more valuable predators fished for human consumption. The pelagic fishery must be managed carefully to ensure that it does not reduce the productivity of the predatory species. Over the past half-century there is some evidence suggesting that industrial fishing has depleted the topmost links in aquatic food chains (Pauly et al. 1998). The idea of large-scale feeding does not imply that any additional fishing of pelagic fish will take place; instead the large-scale feeding can be seen as an alternative to fishmeal production. Otherwise, it could be argued that large-scale feeding might result in overfishing of the prey stocks.

A suitable feeding area that is closed for commercial fishing must be selected where the effects of large-scale feeding can be studied carefully to demonstrate the viability of the method. This would involve measuring, for example, the food intake, growth enhancement, growth efficiency, and biomass of the target species in the feeding area and comparing the increased biological production with the cost of feeding. Initially, the feeding trials must be of intermediate scale, perhaps 10 000 t·year^{-1}, much larger than in the feeding experiment in Stödvarfjördur (Björnsson 1999*a*), but much smaller than the maximum scale set by the total feed supply. Larger scales should only be attempted when the effects of intermediate feeding have been established. In many regulated fisheries, routine surveys are carried out to study the distribution, abundance, diet, and nutritional condition of the most important fish stocks. Also, in some fisheries the commercial vessels are required to enter in their logbooks detailed information about the catch. This information could be useful in finding promising feeding areas where predator abundance is high and food supply low.

It is premature to go into details of legal issues, such as who is going to organize and pay for the large-scale feeding and who is going to harvest the extra yield. However, since most commercial fish stocks are a common resource it seems appropriate that large-scale feeding would become a part of the overall fisheries management. The additional quotas created by feeding could be put up for a bid on the open market. The same research institute that normally monitors the commercial fish stocks could make a feeding plan dictating where and how to feed. A contract could be made with the fishing company that can provide the feed and carry out the feeding at the lowest price. The institute could carry out inspection of the contract work and update the feeding and harvesting plan. Periodically the feeding areas would be opened for fishing to the holders of the additional quotas. The value of these additional quotas would be higher than the normal quotas owing to higher concentrations of well-fed fish at known locations.

To consider the idea of large-scale feeding in more detail,

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the Icelandic cod stock is taken as an example. The benefits from large-scale feeding of the Icelandic cod stock may be threefold: increased yield of cod, decreased predation on valuable species, and decreased cost of fishing. Enhanced food availability as a result of large-scale feeding may increase the annual production and yield of the stock by (*i*) increasing growth rate of individual fish (Magnússon and Pálsson 1989; Björnsson 1999*a*, 1999*b*), (*ii*) increasing fecundity (Kjesbu et al. 1998; Marshall et al. 1999; Yaragina and Marshall 2000), and (*iii*) reducing natural mortality (Lambert and Dutil 2000; Dutil and Lambert 2000). The Icelandic cod stock consumes large amounts of valuable species (Pálsson 1983, 1997*a*). This amount could be reduced if alternative feed is provided. Finally, the catch per unit effort will increase if large numbers of cod can be gathered in a limited area by conditional feeding (Björnsson 1999*a*; Alfredsen 2000).

The marine ecosystem in Iceland

Physical conditions

Iceland (103 000 km^2) is surrounded by rich fishing grounds, most of them within the depth range 0–500 m (212 000 km^2). The areas between the depth contours 0–100, 100–200, 200–300, 300–400, and 400–500 m are approximately 41 000, 69 000, 51 000, 24 000, and 27 000 km^2, respectively (Hilmar Helgason, Icelandic Hydrographic Service, Reykjavík, Iceland, personal communication).

The warm North Atlantic current pushes against the south coast and flows north along the west coast and then eastward off the north coast where it mixes with cold water coming from the north. The annual temperature at a depth of 100 m is highest off the south coast, 6–8°C, gradually declining clockwise around the island reaching a minimum of 2–4°C off the east coast (Fig. 1). As the optimal temperature for growth of adult cod is 6–8°C (Björnsson et al. 2001), the greatest growth potential of cod is off the south coast of Iceland, provided that enough food is available.

Fish and invertebrate stocks

Cod is by far the largest and most valuable demersal fish stock in Icelandic waters. The long-term yield of cod, 372 000 t·year^{-1}, is similar to the yield of all other demersal species in Icelandic waters put together (Table 1). The cod stock is distributed all around Iceland, mostly at depths less than 500 m (Fig. 2*a*); redfish (*Sebastes* spp.) is mostly found deep off the south and west coasts, seithe (*Pollachius virens* (L.)) and haddock (*Melanogrammus aeglefinus* (L.)) off the south and west coasts at depths less than 500 m, and Greenland halibut (*Reinhardtius hippoglossoides* (Walbaum)) in deep water off the east, north, and west coasts of Iceland.

The two most important invertebrate stocks are northern shrimp (*Pandalus borealis* Krøyer) and *Nephrops* (*Nephrops norvegicus* (L.)). Northern shrimp is distributed both inshore (<200 m) and offshore (200–700 m), mostly off the north coast (Fig. 2*b*). In recent years the annual catches have been about 10 000 and 50 000 t in the inshore and offshore shrimp fisheries, respectively (Anonymous 2000*b*). Cod is thought to be the main predator of both inshore and offshore shrimp (Skúladóttir 1994) and it has been suggested that the size of the cod stock may determine the stock size and yield of northern shrimp in Icelandic waters (Stefánsson et al. 1994).

Nephrops is a small stock distributed off the south coast at a depth of 100–300 m (Fig. 2*c*). In recent years the annual catch of *Nephrops* has been 1000–2000 t (Anonymous 2000*b*). The market price of this species is among the highest for all landed species in Iceland, about \$3·kg^{-1} (\$U.S.) whole. Cod is thought to be the main predator of *Nephrops* (Eiríksson 1993).

There are four major pelagic fish stocks exploited by the Icelandic fishing fleet: capelin (*Mallotus villosus* (Müller)), Icelandic summer spawning herring (*Clupea harengus* L.), Atlanto-Scandian herring, and blue whiting (*Micromesistius poutassou* (Risso)). Capelin, usually with a spawning stock biomass of 1 000 000 – 2 000 000 t (Anonymous 2000*b*), is the most important prey of the Icelandic cod stock and an important prey of many other fish stocks (Pálsson 1997*a*). For much of the year, from May to December, most of the adult capelin stock is distributed far north of Iceland (Vilhjálmsson 1994) with limited overlap with the Icelandic cod stock (Fig. 2*d*). In January–March, when the spawning stock moves inshore and migrates to the south and west coasts, it falls easy prey to cod and most other large predators in the area. After spawning, much of the dead or dying capelin is consumed by cod and other demersal predators. The Icelandic capelin fishery is managed in such a way as to leave at least 400 000 t to spawn.

Icelandic summer-spawning herring spawn off the southwest coast, and have exhibited a spawning stock of 500 000 t in recent years (Anonymous 2000*b*). The juveniles live close to the coast all around Iceland, whereas most of the catches of adult herring are taken near the east and west coasts (Fig. 2*e*) (Jakobsson and Stefánsson 1999). Herring constitutes only a small part of the cod diet (Pálsson 1997*a*). The Atlanto-Scandian herring, with a spawning stock of 7 000 000 – 9 000 000 t in recent years (Anonymous 2000*b*), spawns in spring near the coast of Norway; the juveniles live in the Barents sea and the adult fish feed in a large area between Norway and Iceland (Vilhjálmsson 1997). In recent years the catches by the Icelandic fishing vessels have been taken more than 200 nautical miles off the east coast of Iceland (Fig. 2*e*).

Blue whiting, with a total biomass of 5 000 000 – 8 000 000 t in recent years (Anonymous 2000*a*), spawns in March–April around the Faroe Islands. The fishable part of the stock is found over a wide area between Iceland, Norway, and Scotland. Most of the catches by the Icelandic fishing fleet of blue whiting have been taken 50–150 nautical miles off the southeast coast of Iceland (Fig. 2*f*).

Cod—the predator

The Icelandic cod stock

The main spawning of cod takes place in April on the shallow banks close to the southwest coast of Iceland. The eggs, larvae, and fry drift with the clockwise current and most of the juveniles settle off the northwest, north, and east coasts of Iceland from August to October. For the first few years the immature cod are rather localized, but when they become mature, 5–8 years old, most of them migrate from the nursery area north of Iceland to the spawning grounds

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Fig. 1. ●, mean annual temperature around Iceland in the period 1971–1995 at a depth of 100 m at locations A–H, shown with the 200-m depth contour on the inserted map. The two thick lines on the graph, above and below the mean annual temperature, indicate the mean temperature in summer (August) and winter (February), respectively. The thin lines show the lowest and highest values measured during the recording period. Calculations were based on the quarterly hydrographic surveys made by the Marine Research Institute in Iceland. For further orientation of the inserted map see Fig. 2.

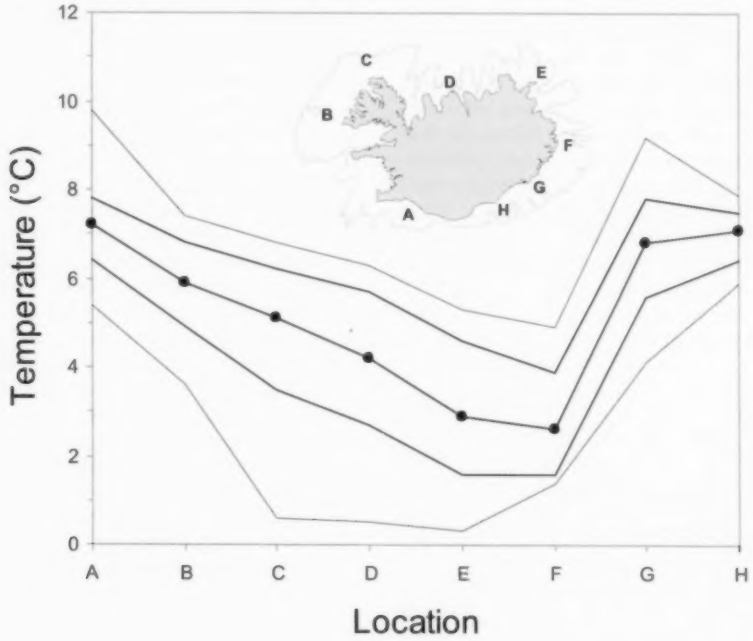

Table 1. Average annual catches of demersal species in Icelandic waters in kilotonnes (kt) (based on Anonymous 2000*b*).

Species	Catches (kt)	Reference years
Cod (*Gadus morhua*)	372	1950–1999
Redfish (*Sebastes* spp.)	87	1969–1999
Seithe (*Pollachius virens*)	70	1950–1999
Northern shrimp (*Pandalus borealis*)	60	1992–1999
Haddock (*Melanogrammus aeglefinus*)	60	1950–1999
Greenland halibut (*Reinhardtius hippoglossoides*)	30	1980–1999
Wolffish (*Anarhichas lupus*)	15	1950–1999
Plaice (*Pleuronectes platessa*)	10	1992–1999
Tusk (*Brosme brosme*)	6	1992–1999
Dab (*Limanda limanda*)	5	1992–1999
Ling (*Molva molva*)	4	1992–1999
Long rough dab (*Hippoglossoides platessoides*)	4	1992–1999
Blue ling (*Molva dypterygia*)	2	1992–1999
Witch (*Glyptocephalus cynoglossus*)	2	1992–1999
Nephrops (*Nephrops norvegicus*)	2	1992–1999
Lemon sole (*Microstomus kitt*)	1	1992–1999
Halibut (*Hippoglossus hippoglossus*)	1	1992–1999

near the southwest coast (Jónsson 1992). During the main feeding season, from May to November, the smaller cod tend to concentrate at a depth less than 150 m but the larger cod prefer deeper waters (Pálsson 1980; Sigurdsson et al. 1997). In recent years most of the commercial catches of cod have been taken off the west, southwest, and south coasts in February–May and off the northwest and southeast coasts in June–January (Sjómanna Almanak 1994–2000). Before 1990, there were also large catches of cod off the north and the northeast coasts (Sigfús Schopka, Marine Research Institute, Reykjavík, Iceland, personal communication).

The food requirement of the cod stock is enormous, 1 000 000 – 2 000 000 t (Björnsson 1997). The fishable part of the stock preys mostly upon other fish, especially capelin

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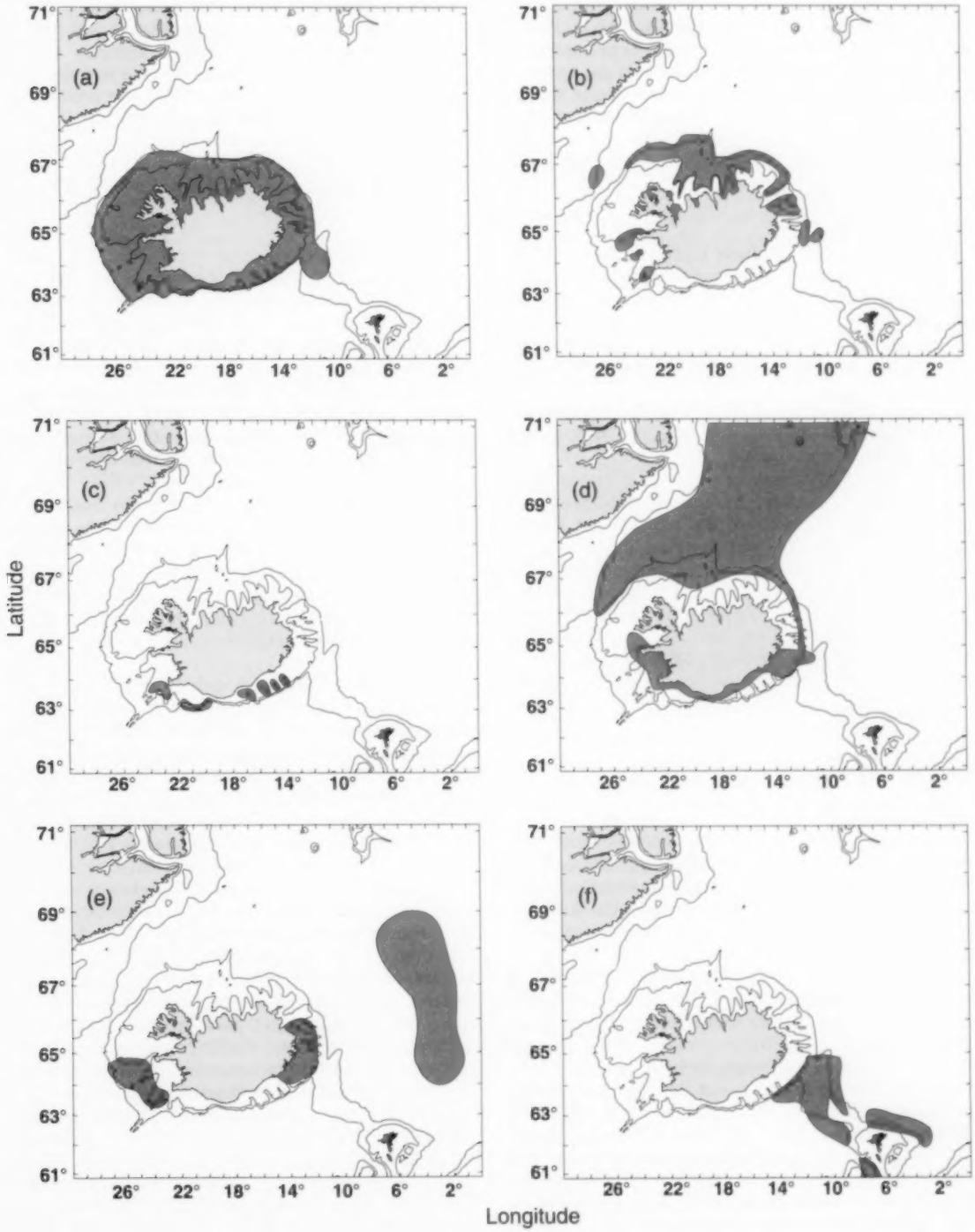
Fig. 2. Distributions of (*a*) cod, (*b*) northern shrimp, (*c*) *Nephrops*, (*d*) capelin, (*e*) herring, and (*f*) blue whiting in Icelandic waters (based on the distributions of commercial catches given in Sjómanna Almanak (1994–2000)). Distributions from the Icelandic groundfish surveys (Pálsson and Stefánsson 1991; Jónsson et al. 1995; Sigurdsson et al. 1997) and Icelandic Directorate of Fisheries database. Land is shown as light grey and the depth contours at 200 and 500 m as thin lines.



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(Pálsson 1983). The main diet is thought to be capelin (49%), redfish (*Sebastes marinus* (L.)) (5%), cod (4%), blue whiting (3%), long rough dab (*Hippoglossoides platessoides* (Bloch)) (2%), wolffish (*Anarhichas lupus* L.) (2%), haddock (2%), herring (1%), sandeel (*Ammodytes* spp.) (1%), northern shrimp (3%), and euphausids (2%) (Pálsson 1997*a*). However, since disproportionately large numbers of cod stomachs were sampled in March, during the spawning migration of capelin, the importance of capelin in the cod diet may have been overestimated and the importance of the other species underestimated (Höskuldur Björnsson, Marine Research Institute, Reykjavík, Iceland, personal communication).

Feeding frequency

It is well known that the optimal feeding frequency of fish increases with temperature and decreases with size. Stomach evacuation time of cod decreases with temperature (dos Santos and Jobling 1991) and increases with particle size (dos Santos and Jobling 1988) and meal size (dos Santos and Jobling 1991). Cod, weighing about 800 g, digested one 16-g herring (2% of body weight) in five days at 4°C. However, five days after consuming meals of one 16-g capelin and three 16-g capelin at 2°C, 10 and 25% of the respective meals remained in the stomach.

One important characteristic of cod is its ability to gorge itself when food is abundant. The maximum stomach content of wild cod is 20–30% of the total weight (Ólafur Karvel Pálsson, Marine Research Institute, Reykjavík, Iceland, personal communication), whereas the long-term maximum food intake at 4°C is only 0.5 and 1.3% of weight per day for 2.2- and 0.9-kg cod, respectively (Björnsson et al. 2001). Thus, it is clear that one maximum meal will fulfil the energy requirement of an adult cod for a long time, at least for one or two weeks at low temperatures. In large-scale feeding, it may therefore be sufficient to release feed once a week in each feeding area.

Available food resource

Catches of prey fishes

For large-scale feeding to be economically feasible, it is necessary to have access to large quantities of inexpensive, high-quality feed and an efficient feeding technique. The most suitable feed for large-scale feeding of the Icelandic cod stock is undoubtedly fresh capelin, herring, and blue whiting. The average annual catch of capelin during the years 1993–1999 was 905 000 t (Table 2), more than 95% of which was sold to fishmeal factories. There are good catches of capelin in the period January–March and usually in June–August and November (Fig. 3).

The Icelandic summer spawning herring is mainly captured from October to January, and the Atlanto-Scandian spring spawning herring in May and June (Fig. 3). The annual landings in Iceland of the former stock have been about 100 000 t for the last decade and about 200 000 t of the latter stock in recent years (Table 2) after a 15-year moratorium and severe catch restrictions during 1985–1994. The total catch of the Atlanto-Scandian herring and 40% of the Icelandic herring catches were sold to fishmeal factories. Annual catches of blue whiting have increased dramatically from <1000 to 160 000 t in the period 1996–1999 (Table 2). Most of the catch has been taken in April–May and July–November (Fig. 3) and virtually all of it sold to fishmeal factories.

During the period 1996–1999 there were 45–48 weeks of the year with catches of capelin, herring and blue whiting above 1000 t and 29–36 weeks of the year with catches above 10 000 t (Table 3), which indicates that there is access to large quantities of inexpensive feed for most of the year. Cod is far more valuable than capelin, herring, and blue whiting. In the period 1995–1998 the average price per landed kilogram of cod was 10–14 times as high as the price of the three pelagic species, but in 1999 the difference was 22- to 24-fold (Table 4).

Quality of feed

The selected diet must be of proper particle size and nutritional value to ensure high growth rate and low feed conversion ratio. The weights of individual landed capelin, blue whiting, and herring are 10–30, 80–120, and 200–400 g, respectively. These prey can be consumed whole by cod larger than 30, 40, and 60 cm, respectively. The target size of cod in large-scale feeding will most likely be above 40 cm, i.e., when they have become predominantly piscivorous (Pálsson 1983), highly mobile, and have relatively low risk of cannibalism and predation (Pálsson 1983; Otterå et al. 1999). Therefore, capelin and blue whiting can be given whole, whereas much of the herring would have to be chopped into 5–10 pieces prior to feeding. The cut must be clean as tearing or crushing may lower the nutritional value of the herring and pollute the feeding area. Suitable cutting machines are already on the market (Sigurjón Arason, Icelandic Fisheries Laboratories, Reykjavík, Iceland, personal communication).

Capelin, blue whiting, and herring are natural prey of cod. They all have a relatively high protein content (11–18%) but seasonally variable fat content (2–25%). The fat content of capelin ranges between 10 and 17% from July to January and then decreases to 2% in April (Vilhjálmsson 1994). The fat content of Icelandic summer spawning herring ranges between 8 and 17% from July to October (Jakob Jakobsson, Marine Research Institute, Reykjavík, Iceland, personal communication), whereas it ranges between 10 and 25% from April to July for the Atlanto-Scandian spring spawning herring (Slotte 1996). The fat content of the Atlanto-Scandian herring ranges between 10–15% in May and June when most of it is fished by Icelandic vessels. The mean fat content of blue whiting ranges from 2% in May to 6% in October (Jón Ingi Ingimarsson, Icelandic Fisheries Laboratories, Reykjavík, Iceland, personal communication). In the autumn and early winter the fat content of capelin and herring may be above the optimum for cod and thus it would be desirable to include blue whiting in the diet.

Growth rate of cod is not sensitive to changes in fat content of the diet. Experimental feeding of 2-kg cod for nine months on maximum rations of natural prey showed no difference in growth rate (0.261–0.299 %·day^{-1}) with different diets of (*i*) fat capelin (16.6% fat, 14.6% protein), (*ii*) lean capelin (4.3% fat, 14.0% protein), and (*iii*) shrimp (3.4% fat, 16.7% protein), but the feed conversion ratio for (*i*), (*ii*), and (*iii*) was 2.3, 4.2, and 4.3%, respectively

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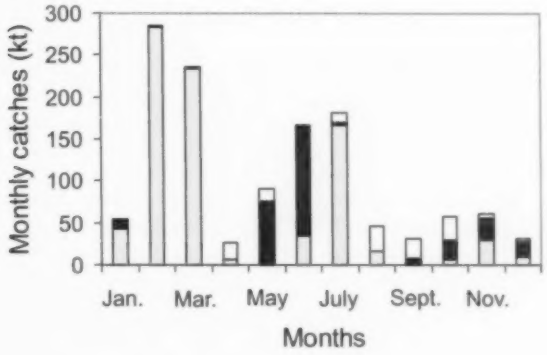
Table 2. Total landings of capelin, herring, and blue whiting in Iceland in recent years (Útvegur 1993–1999).

	Landed catch (kt)						
	1993	1994	1995	1996	1997	1998	1999
Capelin	940	748	707	1178	1314	748	700
Herring (Icelandic)	117	130	110	100	71	77	95
Herring (Atlanto-Scandian)	0	0	174	165	212	193	203
Blue whiting	0	0	<1	<1	10	68	160
Total	1057	878	991	1443	1607	1086	1158

Fig. 3. Monthly landings of capelin (grey), herring (black), and blue whiting (white) in Iceland in kilotonnes (kt), averages for the years 1998 to 1999 (based on Icelandic Directorate of Fisheries database).



(Björnsson 1997). Thus, it is likely that the optimum fat content in the natural cod diet ranges between 10 and 15%.

Possible implementation

Feeding technique

Large-scale feeding would involve transporting capelin, herring, or blue whiting from the location of capture (or the nearest fishing harbour) to the feeding area. The most cost-effective way of feeding would be to contract purse seiners or pelagic trawlers to transport their catch directly to a large school of cod in the designated feeding area. The maximum sailing distance may be as much as 500 nautical miles corresponding to a transportation time of 50 h and thus it is desirable to use vessels with cooling tanks to ensure freshness of feed. Most of the newer purse seiners are equipped with cooling tanks.

A similar technique as used in the feeding experiment in Stödvarfjördur might be applied. In that experiment, a flexible hose was towed behind a boat to flush the feed down to a selected depth (Björnsson 1999*a*). An echosounder and an underwater camera were used to help regulate feeding according to the concentration of fish. A conditioning sound signal was transmitted to concentrate the fish at the time of feeding. During the latter part of the Stödvarfjördur experiment half of the daily feed was put directly overboard. All vessels fishing for capelin, herring, and blue whiting are equipped with powerful fish pumps and thus they would have no difficulty in releasing their catch at given locations.

During the planning phase, the feeding area would be selected according to the distribution and density of cod based on routine groundfish surveys and catch statistics. Subsequently, a more detailed survey would be carried out in the specified area to estimate the feeding capacity of cod and construct an operational feeding plan. Care must be taken not to overfeed to maintain good feed conversion. Before a shipment of feed is allocated to a particular area it must be ensured that there is large enough biomass of cod to consume all the feed released. Cod can consume at least 10% of their body weight when they are hungry. Thus, for a shipload of 500 t of feed a biomass of 5000 t of hungry cod would be required. Although Icelandic cod are sometimes found in large schools (15 000 t, Schopka and Reynisson 1996), normally they have a more disperse distribution and thus initially each shipload may have to be divided between several feeding areas. Regular feeding may, however, attract more and more fish to the feeding areas, thereby increasing the feeding capacity with time. Periodically, the biomass and nutritional condition of the fish in the feeding areas would have to be assessed and the sea floor checked for remains of feed to prevent overfeeding.

In the year 1999 there were 1026, 691, and 307 landings in Iceland of capelin, herring, and blue whiting, respectively. The average catch per landing was 756, 441, and 552 t of capelin, herring, and blue whiting, respectively. However, the weight of catch ranged widely and there were 846 landings below 500 t (Fig. 4). Thus, it would be possible to buy some relatively small shiploads initially in a large-scale feeding trial. Some of the small shiploads may, however, be of poor quality when landed.

Feeding scenarios

The success of large-scale feeding may depend on how, where, and when the feeding is carried out and for what purposes. Five following feeding scenarios are considered for the Icelandic cod stock.

Scenario 1—Feeding of large cod in the distributional area of *Nephrops* (Fig. 2*c*), mainly to reduce predation on this valuable species. As approximately 5 kg of *Nephrops* may be required to produce each kilogram of cod it is clearly wasteful to let cod feed and grow on a species that is 2–3 times more expensive than cod. Less predation by cod would thus increase the maximum sustainable yield of the *Nephrops* stock accordingly. The temperatures in this area are close to the optimal temperature for growth of cod (Björnsson et al. 2001) and any increase in the growth rate of the conditioned cod would be an extra bonus. Any feed not eaten by cod and other predators in the area could be consumed by the *Nephrops* and might thus enhance their growth rate as well.

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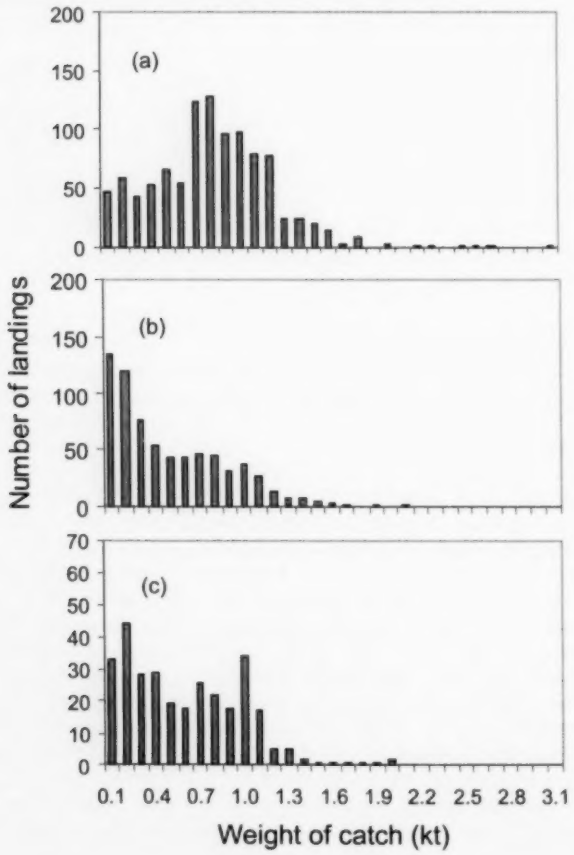
Table 3. Size distribution of weekly landings of capelin, herring, and blue whiting in Iceland in recent years (number of weeks within a given category) (based on Icelandic Directorate of Fisheries database).

	Number of weeks						
Weekly landings (t)	1993	1994	1995	1996	1997	1998	1999
<100	12	9	9	4	3	3	2
100–500	1	1	8	2	1	0	1
500–1000	0	2	1	1	0	2	1
1000–5000	3	6	7	6	7	5	6
5000 – 10 000	6	12	4	3	6	11	13
10 000 – 20 000	7	6	4	13	11	15	13
20 000 – 50 000	18	10	13	9	13	9	10
>50 000	5	6	6	14	11	7	6

Table 4. The relative price of whole ungutted cod relative to that of capelin, Atlanto-Scandian herring, and blue whiting (Útvegur 1993–1999).

	Relative price						
	1993	1994	1995	1996	1997	1998	1999
Cod/capelin	13.3	13.1	13.4	11.0	12.7	12.4	23.6
Cod/Atlanto-Scandian herring			10.9	12.8	12.7	9.7	22.0
Cod/blue whiting			11.9	13.9	11.4	10.0	22.2

Fig. 4. Size distribution of all individual landings in Iceland 1999 of (*a*) capelin, (*b*) herring, and (*c*) blue whiting in kilotonnes (kt) (based on Icelandic Directorate of Fisheries database).



Scenario 2—Feeding of immature cod to reduce predation on inshore shrimp off the north coast (Fig. 2*b*). It has been observed that periodically, large concentrations of cod wipe out shrimp stocks in local inshore areas in Iceland (Unnur Skúladóttir, Marine Research Institute, Reykjavík, Iceland, personal communication). This predatory activity reduces the economic yield of the cod–shrimp fishery, as shrimp is about 20% more expensive than cod. The amount of feeding would have to be adjusted according to the abundance of cod and the predation intensity in the distributional area of inshore shrimp. The shrimp quota could be increased if cod can be conditioned to eat inexpensive feed instead of shrimp. Increased growth rate and yield per recruit of cod would be an additional gain.

Scenario 3—Feeding of immature inshore cod to increase their growth rate, survival, and yield and to reduce predation on expensive species. This part of the cod stock, mostly located off the north coast (Fig. 2*a*), is often in a poor nutritional condition and their growth rates can thus be increased substantially if enough feed is provided (Björnsson 1999*b*; Björnsson et al. 2001).

Scenario 4—Feeding of a mixture of immature and mature migratory cod on the best fishing locations off the northwest and southeast coasts (Fig. 2*a*) to increase the growth rate and yield of cod and to reduce predation on expensive species. This part of the cod stock composes a large fraction of the total biomass of the stock, often forming large schools capable of consuming large quantities of feed. Even the test scale would have to be large, perhaps several tens of thousands of tonnes per year, for measurable effects on the growth rate of cod. This scenario would only be attempted when other scenarios of smaller scale have been tested sufficiently with positive results.

Scenario 5—Feeding of mature migratory cod on the main

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spawning grounds off the southwest coast (Fig. 2*a*) to increase their growth rate and yield and to reduce predation on expensive species. The first fisheries scientist in Iceland pointed out that there was not enough food for cod on their spawning grounds: "On the spawning grounds there is far from enough food for the enormous amounts of cod; they must spread" (Sæmundsson 1926). The question is whether the migratory behaviour of adult cod (Rose 1993) can be overruled by large-scale feeding so as to maintain a significant part of the stock near the spawning grounds throughout the year.

It is stressed that each scenario must be tested initially at an intermediate scale and later on at a full scale with careful monitoring of the effects of feeding on cod and other fish and invertebrates in the feeding area.

Harvesting technique

The optimal harvesting time of the conditioned cod would be in autumn and early winter. The main growing season is in summer after the spawning season. During heavy feeding in early summer the fillet quality of cod is low (Love 1975) and the market price of cod tends to be highest in autumn and early winter (Útvegur 1993–1999). To optimise the feed conversion and yield, the fish must be caught before they channel too much energy into gonads (Eliassen and Vahl 1982). Fidelity to the feeding locations may be high during the summer months when the food requirement and growth potential is high and liver index still increasing. However, in autumn the cod may begin to leave the feeding locations as was observed in the Stödvarfjördur experiment (Björnsson 1999*a*).

Of the traditional fishing methods, gillnetting may be the most suitable technique to harvest the conditioned cod. It is very size selective, leaving the small and immature fish unharmed for the next growing season. By carefully selecting the mesh size it may be possible to optimise the harvest size of the fish. The long-line is not as size selective as the gillnet and will thus do a lot of damage to the small fish. The bottom trawl, which is dragged along the bottom, will cause much more disturbance to the feeding area than the gillnets and may also be harmful to the small fish.

In autumn the gillnets could be set in an area surrounding the feeding area to remove the conditioned fish leaving the feast. The fish in the best nutritional condition are likely to leave earlier than the fish in the poorest condition and the immature fish may not leave the feeding area all year round. This strategy may optimise the harvesting of the conditioned fish by removing only fish that have reached certain minimum size (>4 kg) without disturbing the normal feeding routine in the nearby feeding area. The conditioned cod not caught before the spawning season will have high egg production and egg quality, which may enhance the survival of their larvae (Marshall et al. 1999). After the spawning season the conditioned cod are likely to find their way back to the feeding area.

There is no doubt that the Icelandic fishing fleet could harvest any enhanced fish production, as its fishing capacity is much greater than the total allowable catch. Increased biomass of fish stocks as a result of large-scale feeding is likely to increase the catch per unit effort and thus reduce the cost of fishing.

Possible ecological consequences

Feed conversion

In laboratory experiments 2–3 kg of capelin are required to produce each kilogram of cod (Björnsson et al. 2001), but in nature the feed conversion ratio of cod may be closer to 4. In recent years, the biomass (B) of the fishable part of the Icelandic cod stock has been about 800 000 t and the annual yield (Y) about 200 000 t (Anonymous 2000*b*). To keep things simple it is assumed that natural mortality (M) is 150 000 t (18.75% of B) and the total fish production ($P = Y + M$) 350 000 t. Assuming a feed conversion ratio of 4, the total food consumption (C) would be 1 400 000 t (Fig. 5), which is the same order of magnitude as the annual Icelandic catch of capelin, herring and blue whiting together, the potential feed for large-scale feeding.

The ecological consequences of annual feeding of 500 000 t of capelin, herring, and blue whiting are considered using simple calculations for three different scenarios:

Scenario 1—Large-scale feeding has no effects on predation on wild prey, feed conversion ratio, or natural mortality, and the feed provided would be an addition to the total consumption of wild prey. Then annually the 500 000 t of additional feed would be converted to 125 000 t of cod owing to increased growth rate.

Scenario 2—Large-scale feeding replaces the wild prey of cod without any change in growth rate or natural mortality. The yield of the cod stock would remain unchanged but its consumption of wild prey would be reduced by 500 000 t annually. If 20% of these prey were valuable fish and invertebrates (Pálsson 1997*a*), the increase in yield of other fish stocks than cod might be equivalent to the economic value of roughly 100 000 t of cod.

Scenario 3—All cod conditioned to large-scale feeding consume only the feed provided (no wild prey), natural mortality is unchanged, but their annual weight gain per biomass is 80% higher than for the unconditioned cod (slightly less than what was found in the Stödvarfjördur feeding experiment). If, for the sake of argument, three quarters of the stock biomass would continue to eat wild prey at the same rate and one quarter would eat the 500 000 t of feed given per year, then the annual yields would be 150 000 and 90 000 t for the unconditioned and conditioned cod, respectively. The conditioned cod would thus eat 43% more and grow 80% more per biomass than the unconditioned cod. The total yield of the cod stock would thus increase by 40 000 t and the predation of wild prey would decrease by 350 000 t as a result of large-scale feeding (Fig. 5). If 20% of the reduced predation is valuable fish and invertebrates, the increase in yield owing to less predation might be equivalent to 70 000 t of cod. The total yield of the demersal fishery might therefore increase by 110 000 t. Experimental feeding of free-ranging cod in an Icelandic fjord indicated that the conditioned fish ate only the food supplied and not the wild prey in the area (Björnsson 1999*a*), thus supporting scenario 3.

Even though the three scenarios are quite different the calculations all indicate that the annual yield of Icelandic cod and other valuable species can be increased by about

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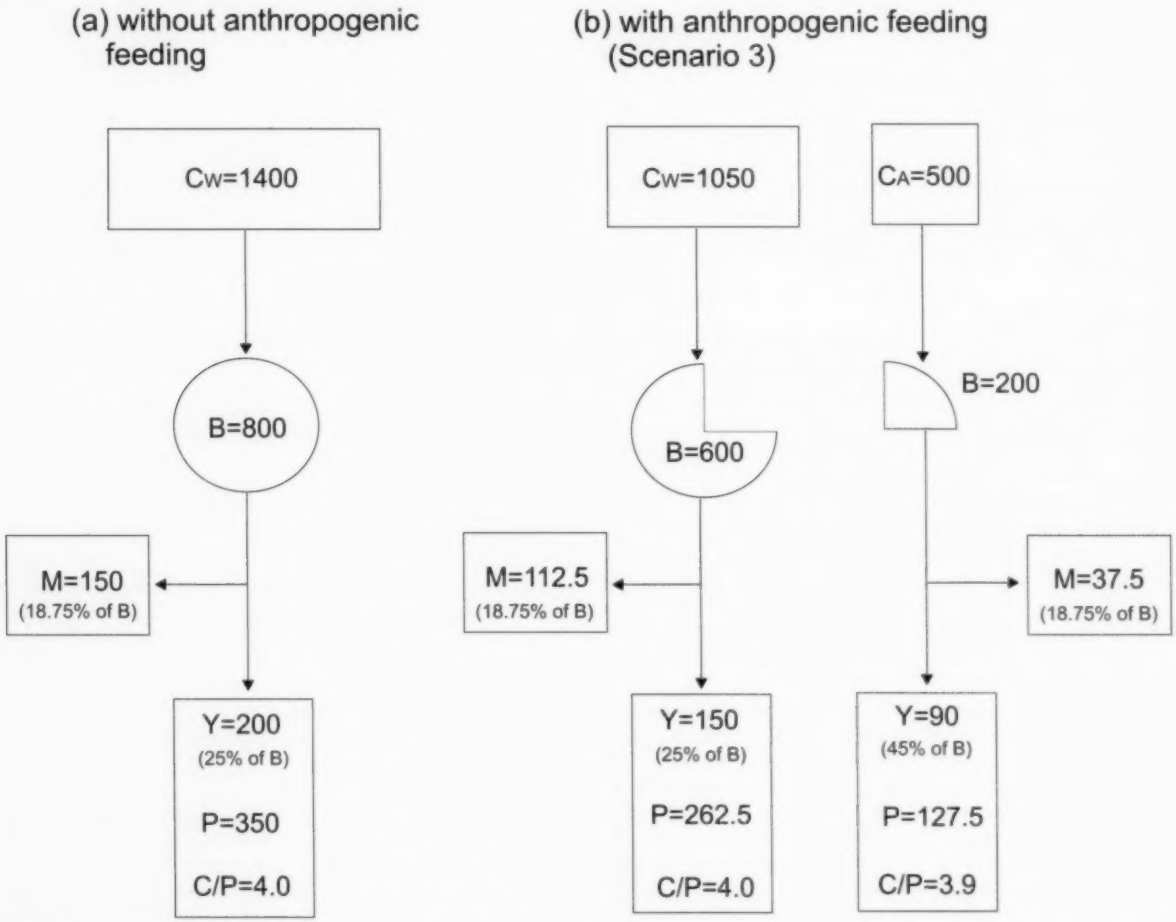
Fig. 5. Feed conversion in the Icelandic cod stock (*a*) without and (*b*) with anthropogenic feeding of 500 000 t·year^{-1} according to scenario 3 (see Possible ecological consequences). C_W, annual food consumption of wild prey; C_A, annual food consumption of anthropogenic origin; *B*, biomass of cod; *M*, natural mortality per year; *Y*, yield per year; and *P*, production per year ($P = Y + M$). All numbers in thousands of tonnes; *C*/*P* is the feed conversion ratio.



100 000 t by annual feeding of 500 000 t. It is stressed that these basic assumptions are simplifications that must be rigorously tested in a field experiment designed to study the economics of large-scale feeding. For example, the yield would be less if some of the feed is not eaten by cod or other valuable species and the yield would be more if (*i*) natural mortality of the conditioned cod decreases with increased food availability, and (*ii*) if the low-priced prey not consumed by conditioned cod according to scenario 3 (280 000 t·year^{-1}) will be consumed by the unconditioned cod. It is beyond the scope of this paper to go into detailed modelling of the ecological effects of large-scale feeding, but such exercises are encouraged.

Migratory behaviour

Cod above 40 cm are very mobile and migratory by nature (Rose 1993; Jónsson 1996). Four- and five-year-old immature cod joined the mature post-spawning fish 180 nautical miles (330 km) off the east coast of Newfoundland to migrate in large size-structured aggregations to feeding areas on the continental shelf. During migration, fish spacing appeared to maximize search volumes while maintaining visual contact (Rose 1993). The migratory route from the nursery area off the north coast of Iceland to the main spawning area off the southwest coast is about 360 nautical miles (670 km).

Distribution of natural prey species can affect the migratory route of cod to some extent (Rose 1993; Lilly 1994; Pálsson et al. 1997). By intercepting cod on their feeding migration with regular releases of feed, it may be possible to build up a large biomass of conditioned cod in a limited area. In April–May, near the end of the spawning season, the post-spawning cod are likely to be very hungry and highly motivated to feed as was found in the Stödvarfjördur experiment (Björnsson 1999*a*). Post-spawning cod in a poor nutritional condition show a marked growth spurt on return to good feeding conditions (Pedersen and Jobling 1989). Therefore, April–May is probably the most effective time to

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condition Icelandic cod to anthropogenic feeding and this strategy will make full use of the warmest months of the year when the growth potential is highest (Björnsson et al. 2001; Björnsson and Steinarsson[1]).

Cod experiencing food "falling from the sky" may alter their vertical migration pattern. Usually the best catches of cod come in benthic trawls, but sometimes large catches of cod are obtained by pelagic trawls when the cod are feeding on pelagic prey. There is a tendency for cod catches to increase in benthic trawls and decrease in pelagic trawls with increased stomach fullness index (Pálsson 1985), suggesting that cod feeding pelagically swim to the bottom when they are full. At the start of each feeding session in the Stödvarfjördur experiment, cod were found near the bottom but ascended rapidly at the sound of the boat and the feed signal. When the feed was put directly overboard, cod gathered in a dense shoal 5–10 m under the boat (Björnsson 1999*a*). This indicates that conditioned cod will ascend to feed and then descend to the bottom to digest.

Discussion

It may seem contradictory to first catch capelin, which is the main prey of cod, and then put it back in the sea as feed for the cod stock. However, for a large part of the year the adult capelin stock is outside the distributional area of the cod stock (Vilhjálmsson 1994). Even during the spawning migration in January–March there are large areas where no capelin is found in cod stomachs (Pálsson and Björnsson 1993; Pálsson 1997*b*; Pálsson et al. 1997). Lack of capelin for a large part of the year may result in starvation, reduced growth, cannibalism, and predation on expensive prey, such as haddock, redfish, shrimp, and *Nephrops*. Hunting for live prey also requires more energy and may be less successful than feeding on dead prey supplied at predictable time and location. Furthermore, virtually all the catch of Atlanto-Scandian herring and blue whiting is taken outside the distributional area of cod.

It is clearly of utmost importance to establish whether the growth and thus yield of a predatory fish stock is food-limited before large-scale feeding is to be implemented. A supporting argument for food limitation is that well-fed cod in captivity grow much faster than wild cod at a given temperature. The average length increment of cod reared in a sea pen at the east coast of Iceland at 2–6°C was 17 cm·year^{-1} compared to 10 cm·year^{-1} for wild cod of comparable size in the area (Björnsson 1999*b*). This corresponded to more than a doubling in the growth of gutted weight, from 0.6 to 1.5 kg·year^{-1}. In a growth experiment in large tanks at 6–8°C cod grew on the average from 49.2 to 70.9 cm and the mean weight increased from 1.2 to 5.0 kg in one year (B. Björnsson, unpublished data). In comparison, the mean weight of 3- and 7-year-old cod in the warm waters south of Iceland in the period 1985–1996 was 1.0 and 5.0 kg, respectively (Jónsson et al. 1997), which gives an indication of the large unused growth potential of the Icelandic cod stock.

Regular feeding of wild, free-ranging cod in an Icelandic fjord, Stödvarfjördur, demonstrated a substantial increase in growth rate of the conditioned cod. In two adjacent fjords and also in Stödvarfjördur prior to the feeding, more than 99% of the cod had livers smaller than 8% of gutted weight. In samples from the feeding areas in Stödvarfjördur, 30 to 60% of the cod had livers larger than 8% of gutted weight. These cod were defined as conditioned fish, some of them with livers as large as 20% of gutted weight. Apparently, cod with smaller livers than 8% had not (or only for a short time) taken the feed. The growth rate estimated for the conditioned cod was 16 compared to 10 cm·year^{-1} for the unconditioned cod, corresponding to approximately doubling in weight gain, from 0.6 to 1.3 kg·year^{-1} in terms of of gutted weight (Björnsson 1999*a*).

The growth rate of Icelandic cod has been found to depend on the size of the capelin stock (Magnússon and Pálsson 1989; Malmberg and Blindheim 1994; Steinarsson and Stefánsson 1996), supporting the hypothesis that the yield of the Icelandic cod stock is food limited. Other cod stocks have also been found to be food limited: Northeast Arctic cod (Yaragina and Marshall 2000), Newfoundland-Labrador cod (Taggart et al. 1994), and northern Gulf of St. Lawrence cod (Dutil et al. 1999).

Questions have been raised as to whether large-scale feeding, intended to reduce predation on expensive species such as *Nephrops* and shrimp, may instead increase the risk of predation by attracting large numbers of predators to the feeding area. However, in the feeding area in Stödvarfjördur it was found that the conditioned cod ate almost nothing but the supplied feed (Björnsson 1999*a*) and laboratory experiments show that cod prefer capelin to shrimp and *Nephrops* (Björnsson, unpublished data). One of the main objectives of a field study would be to assess the effects of large-scale feeding on cannibalism and predation on commercial species by routine sampling of stomach content data and assessment of fish biomass in a feeding area and a non-feeding area used as a control site.

Large-scale feeding is likely to work best for an opportunistic feeder such as cod which will take both live prey, fish, and invertebrates, and dead fish and fish offal from fishing vessels (Sæmundsson 1926). In recent years, about 20% of the total catch of Icelandic cod has been taken by longline which depends on the desire of cod to take bait (herring, squid, and capelin). Catch per unit effort for longline can be large, especially when food is in short supply and cod is capable of consuming cod-shaped fishes up to 50% of its own length (Pálsson 1983).

Cod will readily take dead or moribund prey. In 1954–1956, when the herring stock in the Gulf of St. Lawrence was infected by the fungus *Ichthyosporidium hoferi*, the cod stock was found to consume large quantities of herring (Kohler 1964). Normally, herring is only a small part of the diet but the disease made it an easy prey of cod. Although the cod stock biomass was high at the time, the increased availability of herring was sufficient to increase the growth rate and yield of the cod stock, apparently without any negative effects on the cod stock. A subsequent reduction in cod

[1] B. Björnsson and A. Steinarsson. The food-unlimited growth rate of cod (*Gadus morhua* L.) fed on maximum rations. Unpublished.

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growth was coincident with a subsidence in the herring disease, which greatly diminished the availability of moribund individuals as food (Kohler 1964).

Although large-scale feeding will be directed at the Icelandic cod stock it is unavoidable that some other species of fish will be attracted to the feeding areas. The species composition captured by longline may give some indication of the most likely candidates. In the years 1997–1999, five species of fish amounted to 90% of the Icelandic longline catch: cod (56%), haddock (12%), wolffish (12%), tusk (*Brosme brosme* (Ascanius)) (7%), and ling (*Molva molva* (L.)) (3%) (Útvegur 1993–1999, specifically 1997–1999). These are all valuable species, the price of haddock, wolffish, tusk, and ling relative to the price of cod being 1.17, 0.84, 0.72, and 0.82, respectively (Útvegur 1993–1999, specifically 1997–1999). It is likely that the enhanced food supply will increase the yield of these species as well.

One important advantage of large-scale feeding may be the possibility of carrying out mariculture on a grand scale without harming the environment. Intensive aquaculture in tanks or ponds on land, or in cages close to the coast, may reduce the potential use of the coastal area for recreational purposes. Intensive aquaculture may also result in eutrophication, which may cause harmful algal blooms, oxygen depletion, and destruction of the marine fauna in coastal areas. In intensive aquaculture the high density of fish may increase the risk of diseases and require the use of antibiotics. Also, some undesirable chemicals may be required to prevent algal growth in sea pens. However, by dispensing the feed far enough from shore and in different areas of the open sea, the risk of harmful effects of large-scale feeding would be minimal. It must be pointed out that large-scale feeding may also be used in conjunction with mass production and sea ranching of juveniles of expensive species like halibut (*Hippoglossus hippoglossus* (L.)), to ensure fast growth and high survival.

In conclusion, it is likely that ecological processes will dominate and the food supply will become the main factor in limiting the yield of fish stocks once overfishing has been eliminated. In theory, it seems possible to reduce starvation, cannibalism, and predation on valuable species, and to increase growth rate, survival, and yield by large-scale feeding of a predatory fish stock. The case study of the Icelandic cod stock indicates that many requirements for successful feeding of that stock are met. Future studies must establish how much the yield of some valuable fish stocks can be enhanced and how much the cost of fishing can be reduced. If the results are positive, large-scale feeding may be considered as an important tool for fisheries management, capable of reducing the negative effects associated with temporary and long-term starvation. It is hoped that these contemplations about large-scale feeding of a predatory fish stock may be of help in the search for future means to increase the economic yield from the sea. Hopefully there will be opportunities to put these ideas to rigorous tests.

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DISCUSSION

Tripping over spatial scales: a comment on Guay et al. (2000)[1]

John G. Williams

Abstract: Guay et al. (2000. Can. J. Fish. Aquat. Sci. **57**: 2065–2075) report a test of numerical habitat models (NHMs) that combine two-dimensional hydrodynamic modeling of the depth and velocity fields of a stream reach with simple biological models. The hydrodynamic model was tested with field data from randomly chosen points in the stream, and the overall models were tested with observations of fish in a "verification" section of the stream. This is a proper procedure, but the execution and interpretation of the test seem flawed, largely by a misunderstanding of the spatial scales appropriate. The NHMs used by Guay et al. make predictions for patches or "tiles" at a scale of 1–25 m^2; the hydrodynamic component of the NHMs needs to be tested at the same spatial scale.

Résumé : Guay et al. (2000. J. Can. Sci. Halieut. Aquat. **57**: 2065–2075) présentent un test pour éprouver des modèles numériques de l'habitat (NHM) qui combinent une modélisation hydrodynamique bi-dimensionnelle des champs de profondeur et de vitesse du courant dans une section de cours d'eau avec des modèles biologiques simples. Le modèle hydrodynamique a été éprouvé à l'aide de données de terrain provenant de points choisis aléatoirement dans le cours d'eau et les modèles généraux l'ont été au moyen d'observations sur les poissons faites dans une section de « vérification » du cours d'eau. C'est là une procédure adéquate, mais l'exécution et l'interprétation du test semblent défectueuses, en grande partie à cause d'une incompréhension des échelles spatiales appropriées. Les NHM utilisés par Guay et al. génèrent des prédictions pour des parcelles ou « tuiles » à une échelle de 1–25 m^2; la composante hydrodynamique des modèles NHM doit donc être testée à la même échelle spatiale.

[Traduit par la Rédaction]

Guay et al. (2000) report a test of numerical habitat models (NHMs) with field data from randomly chosen points in the stream. As described by Guay et al. (2000), NHMs combine hydrodynamic modeling and biological indices to predict the suitability of "tiles" or patches of stream by "integrat[ing] the predilection of fish for the substrate diameter, the water depth, and the current speed in that tile [citations omitted]. The end result of the NHM is a map describing the habitat quality index assigned to each tile at a given flow rate." NHMs, for example, the physical habitat simulation system (PHABSIM), are typically used for in-stream flow assessment.

As noted by Guay et al. (2000), other published tests of NHMs have compared distributions of fish with predictions of biological suitability, without testing the intermediate results of the hydrodynamic modeling. In contrast, Guay et al. (2000) tested their modeling results against measurements of water depth and velocity, as well as comparing predictions of habitat indices against observations of the distribution of fish. This is the correct approach (Kondolf et al. 2000), although the presentation and discussion of the hydrodynamic test results are rather brief and raise more serious questions about the test of the NHMs and the hydrodynamic modeling.

Guay et al. (2000) applied their models to three adjacent sections of the Sainte-Marguerite River in Quebec totaling 1500 m in length. The reach consists of shallow pools and riffles with an average slope of 0.003 and several bends. The substrate ranges from sand to boulders. Sampling and model calibration were done at flows averaging 3.7 $m^3 \cdot s^{-1}$, about 5% of bankfull; testing was done in similar conditions. The hydrodynamic modeling was based on 9470 measurements of the bed elevation, producing a set of triangular tiles ranging from 1 to 25 m^2. Two different habitat indices were based on estimates of water depth, vertically averaged velocity, and substrate size over 1 m^2 areas centered on a "home rock" where juvenile Atlantic salmon (*Salmo salar*) were observed holding position. Velocity estimates were based on 30 s measurements at 6/10 depth about 5–10 cm upstream from the home rock for 308 fish in two calibration sections. (The accuracy of such estimates is not well studied, but 95% confidence intervals of roughly 20% of the velocity may be

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[1]Comment on paper by J.C. Guay, D. Boisclair, D. Rioux, M. Leclerc, M. Lapointe, and P. Legendre. 2000. Development and validation of numerical habitat models for juveniles of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **57**: 2065–2075.

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appropriate; estimates based on longer measurements at 2/10 and 8/10 depth are more accurate. See Kondolf et al. 2000 for a discussion.) An equal number of points in areas not occupied by fish were selected randomly, and the depth and velocity of the water at those points were estimated using the hydrodynamic model. A "habitat probabilistic index" was based on these model estimates and the empirical estimates at positions occupied by fish; a "habitat suitability index" was based on the empirical estimates (for utilization) and the model estimates for the whole area (for availability). The habitat indices were calibrated using measurements and model predictions from two of the sections. Predictions of the values of the indices for the tiles were tested against the observed distribution of fish in the third, "validation" section, where the water depth and velocity at tiles occupied by fish were estimated using model predictions, not measurements. (The tiles were grouped by the index values into mappable areas for data analysis and presentation, but the maps are highly detailed and no smoothing of the tile values is described, so apparently the testing was done on a tile by tile basis, as suggested by the language quoted above.)

Guay et al. used a two-dimensional hydrodynamic model, which may avoid the spatial sampling problems involved in the use of one-dimensional models in most NHMs (Williams 1996; Kondolf et al. 2000). To test the model, they measured the depth and water velocity (presumably at 6/10 depth for 30 s) at 271 randomly selected points in their study reach at flows ranging from 2 $m^3 \cdot s^{-1}$ to 5.6 $m^3 \cdot s^{-1}$ and ran their model at the appropriate discharge to predict the water depth and vertically averaged velocity at each point. It is critical that the hydrodynamic or hydraulic models used in NHMs be tested against independently collected data. Although such models are well-established tools routinely used in engineering analyses, it is still necessary to test whether the two-dimensional models can estimate the depth and flow fields of natural streams well enough for the NHMs to function as intended. This is partly because the models were developed, and are mainly used, to model phenomena such as flooding that involve fairly large spatial scales. The habitat indices used in NHMs, however, typically apply over fairly small spatial scales; in this case, they are based on depth and velocity data collected at a scale of 1 m^2 or less.

Although model predictions of depth were fair ($r^2 = 0.85$), point predictions of velocity were poor ($r^2 = 0.09$). Guay et al. (2000) nevertheless conclude that "the precision of the hydrodynamic models that we used was judged sufficient for our purposes." The reasons given are not persuasive. Firstly, they assert that the poor results are largely in parts of the stream with higher and lower velocities than the areas mainly used by fish, but they do not present data on the accuracy of model predictions in what they consider the relevant range (a scatter plot would have been useful; alternatively, model–data comparisons could have been presented for the 308 positions occupied by fish). Secondly, they claim that the model "permitted a good representation of the mean, variance, and range of current speed" for the reach. The data in their table 3, however, show that the mean, variance, and range were underestimated by 20, 29, and 26%, respectively; a 20% underestimate of mean velocity seems biologically significant. Moreover, the tendency of the model to underestimate high velocities, noted by Guay et al. (2000), would lead to an underestimate of the availability of habitat with high velocities; this would explain the reported preference (utilization/availability) for unusually high velocities (60–70 $cm \cdot s^{-1}$) that puzzled the authors.

Thirdly, and more importantly, Guay et al. (2000) assert that "[B]iological models do not require that hydrodynamic models predict physical conditions at a specific point in a reach," but rather over areas. This is true if the areas are small enough, but because the model output "is a map describing the habitat quality index assigned to each tile at a given flow rate", it would seem that a decent representation of the velocity (as well of as the depth and substrate) is required within the tiles, not just within the reach. Such an assessment is also necessary in this case because Guay et al. (2000) used estimates from the model for depth and velocity at specific points in the calibration section in developing one of the biological indices (which performed better than the other in their test) and for calculating values for both indices for positions occupied by fish in the validation section.

Guay et al. (2000) do not show how well their model predicts the average depth and velocity within the tiles, although the poor performance with point measurements of velocity is not encouraging. An appropriate test of the model would be to select tiles randomly and take multiple measurements of depth and velocity within the tiles to get empirical estimates of the mean depth and velocity to compare with the model estimates. Empirical estimates of the variance of depth and velocity within the tiles would also be enlightening.

How well a NMH must predict water depth and velocity in order to be useful is a difficult question with no clear answer and probably depends on the purpose of the modeling, as suggested by Tukey (1960). If the model is used for making decisions about how to act, for example, about how to set in-stream flows, then it seems appropriate to ask how the uncertainty in the hydrodynamic modeling may affect the decision in that particular case. If the model is used to develop conclusions, say about "the existence of general rules that define fish distribution patterns" (Boisclair 2001), then other and perhaps more stringent criteria may be in order. In either case, however, it is important to know how the uncertainty in the hydrodynamic modeling propagates through the biological model in the NHN before the precision of the hydrodynamic model is judged sufficient for the purpose.

Dealing appropriately with issues of spatial scale is a critical and difficult problem for in-stream flow modeling that needs to be approached carefully (EPRI 2000). If the objective really is an estimate of the joint distributions of depth, velocity, and substrate over some larger area such as a river reach, than it seems more straightforward to use an openly empirical approach like that of Lamouroux et al. (1995, 1998) rather than a hydrodynamic model.

In summary, Guay et al. (2000) developed biological indices from data collected at a scale of 1 m^2 and applied them to areas of 1–25 m^2, but the ability of two-dimensional models to estimate the depth and flow fields well enough for this kind of modeling remains to be demonstrated. Notwithstanding the points made above, however, Guay et al. (2000) have taken an important step by comparing the predictions of their hydrodynamic model with measurements from randomly selected locations in the channel. Failure to report

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such comparisons has been an unfortunate hallmark of instream flow studies.

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Science on the edge of spatial scales: a reply to the comments of Williams (2001)[1,2]

J.C. Guay, D. Boisclair, M. Leclerc, M. Lapointe, and P. Legendre

Guay et al. (2000) evaluated the ability of a numerical habitat model (NHM) to predict the spatial distribution of juveniles of Atlantic salmon (*Salmo salar*) in a river. The NHM that we used consisted of a hydrodynamic model predicting the physical characteristics (current velocity, water depth, substrate composition) of habitats under any given flow and a biological model assigning an ecological value ranging from 0 (poor habitat) to 1 (excellent habitat) to habitats using their expected physical attributes as independent variables. The main objective of Guay et al. (2000) was to compare the predictions of NHM based on two biological models to the spatial distribution of fish in a river. The new biological model that we developed, the habitat probabilistic index (HPI), predicted a significantly larger fraction of the local variations of fish density ($r^2 = 0.86$) than the traditional habitat suitability index (HSI; $r^2 = 0.39$). Williams (2001) questioned several methodological and fundamental aspects of the work of Guay et al. (2000). The points raised by Williams (2001) about Guay et al. (2000) can be grouped into problems of wording, problems of sampling sufficiency, and problems of spatial scales.

Wording

The NHM used by Guay et al. (2000) partitions the surface area of the reach modelled into a series of triangular subunits. NHM thereby represents the reach modelled as a mosaic of triangular tiles. Guay et al. (2000) mentioned that the end result of the NHM is a map describing the habitat quality index assigned to each tile at a given flow. The assignment of a habitat quality index *to each tile* was used strictly to facilitate both the writing and the reading of our paper. The comments of Williams (2001) about the spatial scales at which our model was developed, implemented, and tested suggest that we should have specified that habitat quality indices were calculated for the six points delimiting each tile (see Fig. 2 in Guay et al. 2000). These points are located at the intersection and in the middle of the sides of each of the triangular tiles making up the grid used to perform our modelling. Maps of areas of the reach having similar habitat quality indices (further referred to as habitat patches) were drawn using these points. In our maps, habitat quality indices ranged from 0 to 1 and were grouped by intervals of 0.1. Each of the ten classes of habitat quality indices was identified in our maps by a different colour shade. Williams (2001) noted that no smoothing procedure to draw our maps of habitat quality indices was described in our paper. No smoothing procedure was described because none was used. All points within a habitat patch were assigned a habitat quality index corresponding to the specified range of habitat quality index for this patch (no point was "smoothed" to become part of a patch). The locations of the limits between areas assigned with different values of habitat quality were determined by linear interpolation between the habitat quality index assigned to the points delimiting the tiles. This interpolation had no major impact on the habitat patches drawn by our modelling because of the high density of points used to perform our simulations.

Sampling sufficiency

Williams (2001) repeatedly questioned the adequacy of our sampling and of the models that we used to estimate or predict the variables required to perform the numerical habitat modelling. Sampling sufficiency and model performance should be judged relative to the objective of our study. For instance, the field measurements of current velocity made to develop our habitat quality indices and to test the predictions of the hydrodynamic model were taken over 30 s at 6/10 water depth. This approach was selected because it represents the average current velocity within a water column (Dingman 1984; Gordon et al. 1992). Williams (2001) emphasized that taking more measures of current velocity (2/10 and 8/10 water depth) for longer periods of time may provide better estimates of this variable. It is clear that taking more measurements of current velocity will increase the precision of estimates of average current velocity (Kondolf et al. 2000). It is also clear that increasing sampling intensity will necessarily require more effort and time in the field. We feel that any suggestion to further increase the already important logistical effort required to develop NHM should

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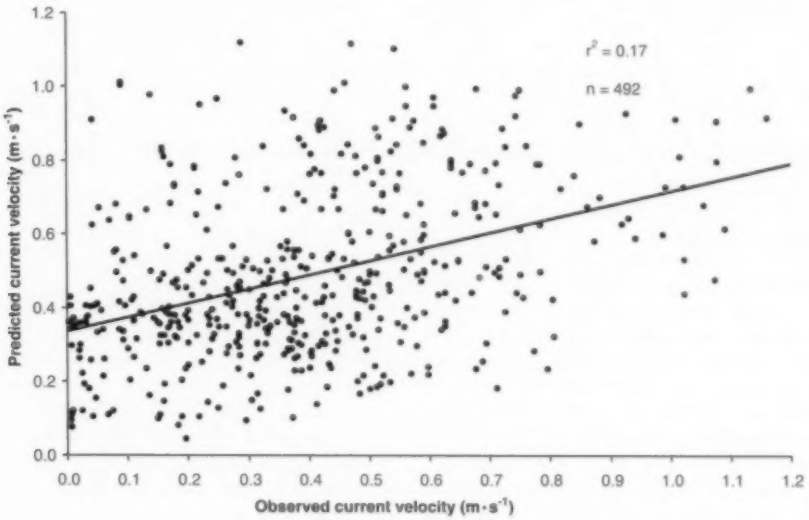
Fig. 1. Relationship between current velocities predicted by the hydrodynamic model used by Guay et al. (2000) at specific points of the Sainte-Marguerite River and observed current velocities at these points. Predictions and observations of current velocities were performed at a flow of 3.2 $m^3 \cdot s^{-1}$.



be justified with very convincing arguments. The strategy of increasing the quantity and the quality of data collected to estimate speed is absolutely correct if the ultimate objective of the sampling is to obtain more accurate data of current velocity. However, our ultimate objective was to model and predict fish habitat and fish distribution. We could not find in the references cited by Williams (2001), or anywhere else, a support for the proposition that the approach that he proposes is better at predicting something useful about fish and their habitats than the approach used by Guay et al. (2000). Furthermore, measuring average current velocity at a given point with a precision of, for instance, 10% appears futile when available hydrodynamic models used to predict current velocity during habitat modelling cannot discriminate instantaneous velocities that vary by an order of magnitude within the range of current velocity observed in the river that we studied. This can be visualized with the relationship between current velocities predicted by the hydrodynamic model for a series of sampling points at a given flow and current speed observed at these points for this flow (Fig. 1). As requested by Williams (2001), we added a total of 221 new data points to develop this relationship to the results presented by Guay et al. (2000). The poor performance of the hydrodynamic model to predict instantaneous current velocity in our study is no doubt related to our use of this model in extreme conditions defined by highly turbulent currents, shallow waters, complex riverbanks, and a riverbed of highly variable roughness on a small spatial scale. The hydrodynamic model that we used has been known to perform better in larger rivers (Leclerc et al.1995, 1996). As such, we recognize that our application of NHM and, in particular, of hydrodynamic models may be "at the edge" of what is scientifically possible with the models presently available. We doubt that increasing the sampling effort to estimate any of the physical variables would significantly affect this performance under the conditions studied. Williams (2001) underlined that Guay et al. (2000) did not show how well the hydrodynamic model predicted the average depth and velocity within the tiles. Unfortunately, we do not have the data to test the performance of the hydrodynamic model at the scale of individual tiles. However, our prediction is that the performance of the hydrodynamic model at the scale of individual tiles would be only marginally better than that found for point estimates.

The strategy used by Guay et al. (2000) was not to improve methods or models to measure or predict current velocity or any other physical variable. Rather, the strategy used was to test if simple and common methods of measurements together with hydrodynamic models currently available could allow us to predict something useful about fish and their habitat. We showed that the level of precision of the approach used to estimate current velocity (and all other variables) was sufficient to explain 86% of the variations in fish density at the scale of habitat patches. We are looking forward to new approaches to measure and model current velocity (or any other variable) that would further improve the predictive power of such NHM.

Spatial scale

The spatial scale for which a model is developed and tested depends on the objective of the modelling. In contrast with the interpretation of Williams (2001), our purpose was not to test the existence of a relationship between habitat quality predicted by NHM and fish density at the scale of 1 m^2 or individual tiles. While we recognize that the wording of our paper could have been more precise, it is not because habitat values are calculated at the scale of specific points, areas of 1 m^2, or tiles that the testing of the relationship between predicted habitat quality and fish density had to be performed at any of these scales. To our knowledge, all fish habitat models use data collected at different spatial scales (points, fish territories, etc.) to assess habitat quality

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Table 1. Minimum, mean, and maximum percentage change in habitat probabilistic index resulting from a 20% or a 50% increase (+) or decrease (–) in water velocity ($m \cdot s^{-1}$), water depth (m), and substrate size (cm).

	Velocity			Depth			Substrate		
	Minimum	Mean	Maximum	Minimum	Mean	Maximum	Minimum	Mean	Maximum
+20%	–0.2	–5.0	–22.9	–0.06	9.5	82.4	–0.01	–2.1	–19.9
–20%	0.4	6.0	22.3	–0.03	–3.1	–133.6	0.01	2.3	19.9
+50%	–0.3	–10.9	–57.5	–0.08	25.7	99.7	–0.03	–4.7	–47.8
–50%	1.2	17.1	53.0	0.14	–3.5	–195.0	0.03	6.4	47.9

at the scale of complete reaches (Boudreau et al. 1996; Heggenes et al. 1996). Consequently, it is not appropriate to conclude from our text that the testing of the relationship between predicted habitat quality and fish density was done (or had to be done) on a tile-by-tile basis. It is also inappropriate to interpret that we tested the prediction of NHM using randomly chosen points (Williams 2001). In fact, the Data analysis section of Guay et al. (2000) described that we tested the prediction of our NHM at the scale of ten habitat patches assigned quality indices ranging from 0 to 1 and grouped by intervals of 0.1. Because our purpose was to test the existence of a relationship between predictions made by NHM and fish density at the scale of habitat patches defined by the NHM, we believe that it is most important that hydrodynamic models should adequately predict physical conditions at this scale. Our study showed that, at the spatial scale of habitat patches, the hydrodynamic model that we used was able to discriminate average current velocities that differed by approximately 20%. Williams (2001) presumed that a 20% error of mean current velocity at the scale of habitat patches might be biologically significant. Although Williams (2001) provides no support for this presumption, our data and models suggest otherwise. We performed a sensitivity analysis to show the effect of modifying water depth, current velocity, or substrate composition by 20% or 50% on our estimates of HPI. The sensitivity analysis consisted of three steps. First, we estimated HPI with 8–12 classes of the three physical variables covering the complete range of these variables and of their combinations in the reach studied. This provided us with 1152 estimates of HPI further referred to as nominal HPI values (12 classes of depth × 12 classes of current velocity × 8 classes of substrate diameter). Second, one of the three physical variables was increased by 20% and the effect of this change on the corresponding nominal HPI values was noted. Third, this physical variable was also decreased by 20% to assess the effect of such a change on nominal values of HPI. The same procedure was used to assess the effect of a 50% increase or decrease of any physical variable. The effect of a 20% or 50% increase or decrease was tested independently for the three key physical variables to assess the relative sensitivity of our HPI model to these variables. These simulations indicated that a 20% and 50% change in current velocity resulted in a mean change of 6% and 17.5% in HPI, respectively (Table 1). Interestingly, for specific combinations of physical variables, a 20% change in water depth could affect HPI by as much as 133%. However, a 20% variation in current velocity and substrate composition never affected HPI by more than 22.9% and 19.9%, respectively. Hence, our sensitivity analysis tends to suggest that our HPI is most sensitive to water depth. This may partly explain why NHM performed relatively well despite the poor performance of hydrodynamic models at predicting current velocity at the scale of points. Taken together, our sensitivity analyses suggest that a 20% error in current velocity would result, at most, in a 23% change in HPI (e.g., at most, a change of HPI value from 0.4 to 0.5). As can be judged from our Results (Fig. 6*b* in Guay et al. 2000), this degree of variation has no effect on our finding of the existence of a strong relationship between the predictions of NHM and fish density at the scale of habitat patches. Williams (2001) suggested that considering the poor precision of available hydrodynamic models on an instantaneous basis, habitat modelling should be performed using an empirical approach such as proposed by Lamouroux et al. (1998). Although this approach appears promising, we believe that it should be tested in a manner similar to that used by Guay et al. (2000) before judging the relative merits of NHM based on empirical and hydrodynamic models.

We can only partly agree with Williams (2001) that the ability of two-dimensional hydrodynamic models to estimate the depth and flow fields well enough for numerical modelling remains to be tested. This evaluation depends on the definition of "well enough" and on the modelling objective (spatial and temporal scales). The only way to evaluate if the precision of hydrodynamic models is sufficient to assess fish habitat quality is to compare the predictions of NHM based on these hydrodynamic models with real fish distribution patterns at the desired scale(s). Although our models were developed using data collected and processed at the scales of 1 m^2 and individual tiles, we have not performed the comparison between predictions of NHM and fish density at these scales because, as we have shown, hydrodynamic models cannot adequately predict physical conditions at these small spatial scales. Furthermore, we do not feel that such comparison is useful in our case. Considering the average density of fish in the river studied (1–3 parrs/100 m^2), we would be correct in predicting that there are no fish in a given area of 1 m^2 in more than 96% of the cases. We are not sure, however, that this sort of prediction has much practical value in a decision-making process. Finally, even if it were possible, we would question the practical utility of predicting habitat quality at the scale of 1 m^2 on the basis that it may be difficult to adopt and implement management decisions on such a small spatial scale. At the scale of habitat patches, however, we found that habitat quality predicted by our NHM explained 86% of variations of fish density. Consequently, our work suggests that NHM allows us to predict something ecologically useful about fish habitats and at a spatial scale that is practically manageable. Hence, we agree with Williams (2001) that the question of the ability of two-

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dimensional hydrodynamic models to estimate key variables at the scales of 1 m^2 or individual tiles remains open.

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a)

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c)

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Where: The Empire Landmark Hotel and Conference Centre
1400 Robson Street, Vancouver, BC Y6G 1B9
Telephone: 800-830-6144

Themes: Climate Change Impacts on Aquatic Ecosystems (CCFFR/SCL)
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W. E. Ricker: Shaping a Science (CCFFR)
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Funding: Graduate students may apply to the Clemens-Rigler Travel Fund.

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